Learned from What *You* Did:
Retrieving Rules Learned by Observation

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Introduction

In daily life many arbitrarily fixed and generally adopted "rules" must be accepted and adequately applied. These rules are very often associations of sensory environmental events (e.g. image, symbol, etc) with particular motor responses or actions. Those rules are defined as "visuo-motor associations". There is often no spatial correspondence between cues and associated movements, and for this reason Wise et al. (Wise et al., 1996; Wise and Murray, 2000) defined them as "non-standard", by opposition to "standard" sensorimotor mapping. The association between the stimulus and the appropriate behaviour is entirely arbitrary, and must therefore be learned or acquired. Different mechanisms can be used to acquire such knowledge, each of which has its own properties in terms of risk and cost for the learner.

If one excludes learning through verbal explanations and instructions, which necessitates language, learning by trial and error and by observation are two mechanisms of particular interest for the development of culture in human infants and adults (Castro and Toro, 2004; Cavalli-Sforza and Feldman, 1983). These two mechanisms share the necessity to associate the perception of a stimulus with a particular behaviour and to take into account the consequence of this behaviour to achieve the learning of a rule. The major difference between these two mechanisms is that the action and its consequence are experienced by the learner himself in the case of learning by trial and error, or by another individual in the case of learning by observation. Arbitrary visuo-motor associations can thus be individually learned from others who already know them. In the first case, the individual endures the positive or negative consequences of his trials. In the latter, the individual is not directly exposed to negative outcomes and only observes the consequences of others' actions. This difference is important in terms of cost for the learner. As Bandura (1977) stated it: "Learning would be exceedingly laborious, not to mention hazardous, if people had to rely solely on the effects of their own actions to inform them what to do. Fortunately, most human behaviour is learned observationally through modelling: from observing others one forms an idea of how new behaviours are performed, and on later occasions this coded information serves as a guide for action." (Bandura & al., 1977). Social/observational learning thus improves human adaptability and allows individuals to acquire a vast store of useful knowledge without incurring the cost of discovering and testing this knowledge themselves (Boyd and Richerson, 1985, 1988; Wise et al., 1996).

From the neural perspective, learning complex arbitrary associative visuo-motor associations (or rules) relies on the formation of neural representations of the relation between visual stimulus and its associated action. Several neuroimaging studies have established that learning arbitrary visuo-motor associations by trial and error engages a large brain network including the frontal-parietal system, the basal ganglia and medial temporal structures (Dieber et al., 1997; Toni and Passingham, 1999; Toni et al., 2001; Eliassen et al., 2003; Law et al., 2005; Brovelli et al., in press). In parallel, various studies have shown that the prefrontal cortex is particularly involved in the storage and retrieval from long-term memory of known visuo-motor rules, or prescribed guides for action (Bunge et al., 2003; Bunge, 2004; Crone et al., 2006; Donohue et al., 2005). However, despite its outstanding scientific interest, the neural bases of learning and retrieval of visuo-motor associations when learned by observation remain surprisingly unexplored.

In the present study, we investigate the neural representations of visuo-motor association retrieval by testing the appealing hypothesis that different brain structures support rule retrieval if previously learned by trial and error or by observation. The retrieval of a visuo-motor rule is defined as the retrieval of the correct action associated to a given abstract visual stimulus. In other words, we indirectly test whether observational learning is mediated by specific neural circuits linking environmental information (visual stimuli) with the re-enactment of another's action to generate internal representations of abstract rules. To do so, eleven adult subjects were asked to learn, prior to the fMRI scanning session, two sets of visuo-motor associations either by trial and error or through the observation of an actor performing the task. Following fMRI acquisition, we compared the brain activations of the subjects when requested to retrieve the associations learned by trial and error or by observation.

Materials and Methods

Participants

Eleven healthy, right-handed volunteers (7 males, 4 females) participated in the study (mean age: 26.3 ± 4.2 years). All subjects were screened to rule out medication use, history of neurological or psychiatric disorders, head trauma, substance abuse, or other serious medical conditions. Written consent was obtained after the procedure had been fully explained. The study was approved by the local Ethics Committee and was conducted in accordance with the Declaration of Helsinki. Volunteers were paid for their participation.

Design and Experimental Conditions

Learning sessions prior to scanning

Prior to fMRI scanning, subjects learned arbitrary associations between abstract visual stimuli (linear segments combined to form white shapes on a black background and motor responses (joystick movements). Each subject had to learn one set of three visuo-motor associations by trial and error and another set by observing an expert actor performing the visuo-motor associations in front of her/him. The order of the two learning sessions was randomised between subjects.

During the trial and error learning session, the visual stimuli were presented on a computer screen in front of the subjects. Motor responses were recorded with a joystick. After presentation of the visual stimulus (1.5 s), the subject had to choose one of the four possible joystick movements (up, down, right or left). The visual feedback (a green/happy or red/sad smiley-like face) then indicated whether the movement was correct or incorrect. The correct stimulus-response associations were kept constant across the experiment. To ensure that participants had perfectly learned the associations, the session ended when the subject had given 4 consecutive correct responses to each of the 3 visual stimuli. A pilot study was conducted on 5 subjects in order to validate this overlearning criterion. A mean of 46,36 trials was necessary to reach the criterion.

During the learning by observation session, subjects had to learn the associations through the observation of an expert individual demonstrating the correct visuo-motor associations. The subjects were seated beside the demonstrator and close enough to observe the visual stimuli on the computer screen and the joystick movement (distance = approximately 50 cm). A pilot study was conducted on 5 subjects, in order to estimate the approximate number of trials repetition necessary to learn the associations. To ensure that the participants had learned perfectly the visuo-motor associations, the session ended when the subjects told the experimenter that they felt sure to perfectly know the associations. It was obviously not possible to check that rules were learned perfectly by observation before the scanning session. Instead, behavioral performances obtained during fMRI scanning were used as a control of learning. A mean of 15,27 trials was necessary to learn the associations.

Scanning session

Stimuli and experimental design

Subjects were scanned about half-an-hour after the learning session. The experiment was built as an event-related paradigm with three trial types (conditions). Each trial started with a fixation cross (1 s), immediately followed by the presentation of the visual stimulus (1.5 s). In the Trial and Error (TE) condition, the visual stimuli pertained to the visuo-motor associations that the subject had learned by trial and error previous to scanning. In the Learning-by-Observation (LeO) condition, the stimuli had been previously associated with a specific movement by observation. A third trial type served as control condition (CONT), in which arrows pointing in one of four directions were used as visual stimuli. The stimulus properties in the control condition were very similar to those in the TE and LeO condition. Subjects were not explicitly informed that the arrow indicated the correct direction of movement. For all conditions, the stimulus presentation was followed by a video sequence of 3 seconds showing the hand of an actor executing a joystick movement. A variable delay between 5 and 12 seconds was introduced between the stimulus and the video presentation to dissociate the BOLD responses produced by the two events. After each movie, the subjects had to judge whether the joystick movement executed by the actor was correct or not. The actor's movement were correct in 50% of the trials. Responses were collected using a two-button computer mouse and the buttons associated with the "correct" and "incorrect" responses were randomized across trials. Subjects performed a total of 40 trials of each of the three conditions, intermixed pseudo-randomly in four runs. Each run consisted of 30 trials (10 of each condition), and the presentation order of runs were randomized between subjects. Behavioural data (accuracy and reaction time) were collected during the scanning sessions. The stimuli were projected onto a screen positioned in the back of the scanner. Subjects could see the video reflected in a mirror (15x9 cm) suspended 10 cm in front of their face and subtending visual angles of 42° horizontally and 32° vertically.

Image acquisition

Images were acquired using a 3-T whole-body imager. For each participant, we first acquired a high-resolution structural T1-weighted anatomical image (inversion-recovery sequence, 1 x 0.75 x 1.22 mm) parallel to the AC-PC plane, covering the whole brain. For functional imaging, we used a T2*-weighted echo-planar sequence at 36 interleaved 3.5-mm-thick axial slices with 1 mm gap (TR = 2400 ms, TE = 35 ms, flip angle = 80°, FOV = 19.2 x 19.2 cm, 64 x 64 matrix of 3 x 3 mm voxels).

Data processing and statistical analysis

Image processing and analysis of fMRI data were conducted with SPM2 software (http://www.fil.ion.ucl.ac.uk/spm/software/spm2/). The first five volumes of each participant's data were discarded to allow for longitudinal relaxation time equilibration. All functional images for each subject were slice-time corrected to a slice acquired half-way through image acquisition in order to correct for temporal differences (up to 2.4 s) between slices acquired early, and those acquired late in the image volume. All volumes were realigned to the first volume to correct for head movement between scans. A mean image was created using the realigned volumes. The mean image was spatially normalized to the standard EPI template given in the SPM software. All images were then spatially normalized using the normalisation parameters determined during the normalization of mean image to EPI template. Data were then smoothed using an 8 mm full width at half maximum isotropic Gaussian kernel to accommodate inter-subject differences in anatomy. Finally, intensity normalization and high-pass filtering (128 s) were applied to the data.

The statistical analysis of the pre-processed event-related BOLD signals was performed using a general linear model (GLM) approach. Since we aimed at dissociating 2 events per trial (the stimulus and video presentation), two regressors were constructed per trial type by convolving the canonical haemodynamic response function (HRF) with delta functions aligned either on the time of stimulus or video presentation. The design matrix contained a total of six regressors (two regressors for each of the three conditions). Since we hypothesized that rule retrieval occurs at stimulus presentation, the significant key differences in brain activity due to the type of learning were searched on the regressors aligned on the stimulus.

The regression parameters (the beta values) were estimated for each subject, and were then taken to the random-effects level. All the fMRI statistics and p values arise from group random-effects analyses. We considered as activated brain regions those clusters of more than 10 contiguous voxels with $p < 0.001$ at the voxel level (uncorrected for multiple comparisons). While this is less rigorous than reporting only those voxels where BOLD response survived Bonferroni correction for multiple comparisons, the exploratory threshold of $p<0.001$ uncorrected has been widely used in previous fMRI studies of subtle cognitive processes.

Results

Eleven subjects participated in the fMRI study. Prior to the scanning session, subjects learned two sets of three arbitrary visuo-motor associations. One set was learned by trial and error and one set by observation of an expert actor performing the task. During the scanning session, the subjects were tested in three different conditions: retrieval of rules learned by trial and error, retrieval of rules learned by observation and a control condition using arrows as stimuli (see methods).

The mean percentage of correct responses for each experimental condition acquired during fMRI scanning confirmed that subjects could perfectly retrieve the visuo-motor rule for all stimuli. There was no significant difference across conditions (TE, LeO and CONT) in reaction times (F (2.768) = 0.238, p>.05), suggesting that task difficulty was comparable in all experimental conditions.

We compared the brain activations associated with the perception of three types of stimuli: 1) stimuli associated to a specific motor action following a rule learned by observation prior to scanning (LeO condition); 2) stimuli associated to a specific motor action following a rule learned by trial and error (TE condition); 3) stimuli associated to an intuitive movement that the subjects had known and used for a long time (arrows, CONT condition) (see methods). As stated above (see 'Data processing and statistical analysis' section), we hypothesized that rule retrieval is triggered by stimulus presentation. For this reason, the significant differences in brain activity due to the type of learning were searched on the regressors aligned on the stimulus.

To reduce unspecific effects related to the retrieval of visuo-motor associations not learned either by trial and error or by observation (i.e., the arrows), we subtracted the brain activity in the control condition from the TE and LeO conditions. We then performed a conjunction analysis between the contrasts 'TE' – 'CONT' and 'LeO' – 'CONT' to explore the brain areas commonly activated both in the 'LeO' and 'TE' conditions. This analysis revealed BOLD signal increases bilaterally in three distinct foci of the lateral prefrontal cortex (BA46; ventral *pars opercularis* BA44; dorsal *pars opercularis* BA44/45), in a bow-like large cluster spreading from the inferior to the superior posterior parietal cortex bilaterally, in the dorsal posterior cingulate gyrus extending dorsally to the pre-SMA, in the posterior ventro-temporal visual areas, and in the thalamus. This network represents areas that activate during the retrieval of associations recently learned either by trial and error or by observation. Finally, to assess which brain areas are specifically involved in rule retrieval after observational learning, we performed a direct comparison between conditions LeO and TE. Significant activations were found in the right prefrontal cortex (*pars triangularis*, BA 45), in the inferior parietal lobule (BA 40) and in the occipital primary visual areas (BA 17/18).

Discussion

Although various aspects of rule retrieval and their neural correlates have been explored in recent studies (Bunge et al., 2003; Crone et al., 2006; Donohue et al., 2005), none have addressed the specific issue of whether the cerebral areas engaged in rule retrieval could be influenced by the way the rule was previously learned. In this study, we manipulated how a visuo-motor rule was learned prior to scanning and investigated its brain correlates during retrieval.

During the scan session, in the TE condition, the prediction of the correct associated movement in order to perform a correct judgement on the subsequent movie necessitated the recall of a visuo-motor association previously learned by trial and error. In the LeO condition, prediction of the correct movement required the recall of a visuo-motor association learned by observation of another individual. By contrast, in the control condition (CONT), prediction of the correct movement did not necessitate the recall of a visuo-motor association learned recently by trial and error or by observation since it was based on the knowledge about the direction of movement indicated by a pointing arrow – a rule learned earlier in life. We used abstract visual stimuli to minimize verbalization (internal speech) effects that could account for differences in brain activations between the TE/LeO conditions and the CONT condition.

Therefore, we argue that differences in brain activations between conditions TE and LeO are exclusively related to type of learning. Acquiring associations by Trial and Error required subjects to learn from errors and correct trials, while in observational learning subjects memorized correct examples only. The training sessions were matched to assure that subjects performed the task during scanning without errors. Indeed, the analysis of behavioural data confirmed that the level of performance and reaction times were statistically identical in all conditions.

Common networks involved in retrieval of rules learned by trial and error and by observation.

The results from the conjunction analysis confirmed the involvement of a brain network composed of the right ventrolateral and anterior prefrontal cortices, pre-SMA, and parietal cortex when retrieving newly acquired rules (Bunge et al., 2003; Bunge, 2004; Crone et al., 2006; Donohue et al., 2005). This is consistent with a role of the inferior frontal junction in the retrieval of actions associated with symbolic cues (Donohue et al., 2005). It also confirms that the posterior medial temporal gyrus plays a general role in storing action knowledge, more specifically in representing arbitrary associations between symbols and associated rules for how to act (Donohue et al., 2005). Classically, this functional interpretation was elaborated on results from studies on the retrieval of appropriate action representations built on the *subject's own* actions during learning. The original contribution of our data is to show that this same network is also recruited when the representation has been built *via* the *observation of another's* actions with the aim of learning. A straightforward interpretation is that during both types of learning, the brain builds an internal model linking an executed or observed action with a visual stimulus and a feedback. The generation of such internal models necessitates taking into account one's own or another's action through the activation of brain areas coding for action execution or observation. Except for the most anterior frontal area (BA46), the activations in the dorsal and ventral part of *pars opercularis* and in the parietal cortex have been consistently reported in studies where subjects execute, observe, imitate or understand actions, intentions or emotions, pretend to use tools, or generate verbs (Buccino et al., 2001; Gazzola et al., 2007; Grèzes et al., 2003; Iacoboni et al., 2005; Jeannerod, 2001; Rizzolatti et al., 1996; Wicker et al., 2003a). These properties led to the claim that these brain areas are core components of the mirror neuron system (MNS) in humans and may be the seat of an action and intention understanding mechanism (Rizzolatti and Craighero, 2004). The mirror system areas are activated not only when an individual performs an action but also when one observes the same action performed by another agent(Gazzola et al., 2006; Iacoboni et al., 2005). In the present study, the prefrontal and parietal regions are activated during abstract stimulus perception and rule retrieval, but also during observation of movies, which demonstrates their role in action observation. Although we did not have an experimental condition to map the brain areas involved in action execution, our results suggest that the role of a subset of the mirror system goes beyond the execution and observation of actions and could be related to the retrieval of visuo-motor rules recently learned by trial and error or by observation. This leads us to the appealing suggestion that a mirror-like system exists and contributes to the construction of rule representation. In the case of trial and error, action executed by the subject to learn the visuo-motor association are stored in his own motor areas, while during learning by observation it is the observed actions of the actor that are stored in the same 'mirror' areas. This interpretation of our findings implies that, in addition to the classically described mirror neurons that fire during the execution and observation of the same or broadly identical motor act (e.g. a joystick movement), a subset of these neurons might be visually triggered by the presentation of an abstract stimulus that has been previously associated to a specific action. This ability might rely on a kind of *mirror activity* of prefrontal areas, more precisely in the ventral and dorsal part of the pars opercularis". As for the understanding of sensations (Keysers et al. 2004), emotions (Wicker et al., 2003b) and pain (Singer et al., 2004), observational learning might thus be supported by a re-enactment of the experience of the model in the observer. Albeit theoretically (Gallese and Goldman, 1998), literature in the field of rule retrieval and learning in general has not been linked to literature on mirror neuron system, here we provide suggestive evidence of a possible role of the MNS in the observational learning of associative rules.

A specific network for the retrieval of rules learned by observation

The observation of abstract stimuli and their association to specific movement guided by a rule learned by observation yielded activation in a network of brain areas comprising the right *pars triangularis (BA 45),* the right inferior parietal lobule and the posterior visual areas. A major difference between the trial and error and observational learning is that trial and error learning relies on a mixture of external and internal information. By contrast, learning by observation primarily requires subjects to attend to external information generated by the other individual's actions and the feedback that is given to him/her. We performed a student t-test on the average percent change in BOLD signal in the right *pars triangularis* during rule retrieval and movie observation. It revealed similar BOLD responses when subjects retrieved the motor action associated with a visual stimulus in the LeO condition and when subjects watched a video sequence of a hand performing a joystick movement. This suggests that the *pars triangularis* is engaged both during observation of action and during the retrieval of the correct movement previously associated with a stimulus by observation of another's action. This is consistent with recent data showing that the right *pars triangularis* is involved in action observation but not in imitation, hence not in execution (Molnar-Szakacs et al., 2005). Because of these properties, authors have suggested that this region should not be considered as part of the mirror system, but rather as related to the suppression of movement execution during action observation and motor imagery (Deiber et al., 1998; Molnar-Szakacs et al., 2006).Alternat, this Our results thus suggest that the mere perception of an abstract stimulus previously associated with a specific movement is sufficient to activate this area and hence that this region plays an important role in storing information about other's actions performed in a given context. One could further propose that this area monitors the flow of information within the fronto-parietal network, to store the information as an internal representation about the actions of the demonstrator in relation with the visual stimulus and the feedback. Interestingly, the rostral part of the IPS has been recently claimed to play a key role in observational learning of complex action sequences by forming representations of the temporal ordering of component actions that are available to guide subsequent performances of these goal directed behaviours (Frey et al., 2006). We extend this finding by showing that this region is also engaged when the level of representation necessary for retrieval of the correct answer is more abstract.

What could explain the specific activation of early visual areas depending on the way the visuo-motor association was learned? Since conditions were identical in terms of complexity of the visual stimuli, we can propose that this activation of the primary visual areas could result from top-down modulations of its activity. Indeed, results of several neuroimaging studies have suggested that a frontal-parietal network controls attention by sending "top-down" signals modulating the activity of the visual cortex during the execution of given tasks (Hopfinger et al., 2000; for review, see Corbetta and Shulman, 2002). In the present study, the retrieval process might necessitate the reactivation of what movement had been observed during learning and the top-down modulation might affect distinct primary visual areas depending on whether the rule was learned in LeO or in a TE context (Vidyasagar and Pigarev, 2007 ; Supèr et al., 2001). In a recent study using magnetoencephalography, Nueuwenhuis et al. showed an increased gamma activity in the early perceptual areas (BA17 and BA18) when labile compared to stabilized memories are recalled (Nueuwenhuis et al., 2008). This result further increases the evidence that the visual system is engaged in tasks beyond visual perception. These tasks include directed attention, working memory maintenance and long-term memory encoding and recall (Jensen et al., 2007).

In summary, from our evidence, we suggest that the mere perception of an abstract visual stimulus that has been previously associated with a motor response by trial and error or by observation of an actor is sufficient to trigger the activation of a set of brain areas typically involved in action observation or execution. This suggests the existence of a common neural system responsible for the storage of stimulus-response mappings learned either by trial and error or by observation of another's actions. Retrieving an abstract visuo-motor rule learned by observation engages the *pars triangularis* of the right prefrontal cortex, reflecting the potential value of other's actions in such context and the need for its privileged processing.

The results of the present study try to bridge the gap between two widely explored cognitive functions: individual learning and action observation and understanding. Visuo-motor individual learning is thought to be mediated by the fronto-striatal system (Wise et al., 2000; Hadj-Bouziane and Boussaoud, 2003), whereas action observation engages the fronto-parietal mirror system. The fact that we can learn both through trial and error and from observation of other's behaviour means that these two systems interact to allow the transfer of other's experience from the fronto-parietal system to the fronto-striatal system. Could the mirror system promote learning by observation? (Gallese and Goldman, 1998). If so, the fronto-striatal and the fronto-parietal systems cooperate to ensure the learning of behavioral patterns via observation of other's actions. To inquire these issues, studies exploring the dynamics of observational learning *during* scanning are now needed, in order to provide a clearer picture of the brain network responsible for our ability to learn via the other's actions.

Bibliography

Bandura A., 1977. Self-efficacy: toward a unifying theory of behavioral change. Psychol. Rev. 84, 191-215.

Boyd R. and Richerson P.J., 1985. Culture and the Evolutionary Process. University of Chicago Press, Chicago.

Boyd R. and Richerson P.J., 1988. An Evolutionary Model of Social Learning: The Effects of Spatial and Temporal Variation. In: Zentall, T.R. and Galef, B.G. (Eds.), Social Learning: A Psychological and Biological Approaches. Erlbaum, Hillsdale NJ, pp. 29-48.

Brovelli A., Laksiri N., Nazarian B., Meunier M., Boussaoud D. (in press). Understanding the Neural Computations of Arbitrary Visuomotor Learning through fMRI and Associative Learning Theory. Cereb. Cortex. PMID: 18033767.

Buccino G., Binkofski F., Fink G.R., Fadiga L., Fogassi L., Gallese V., Seitz R.J., Zilles K., Rizzolatti G., Freund H.J., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur. J. Neurosci. 13, 400-404.

Bunge S.A., 2004. How we use rules to select actions: a review of evidence from cognitive neuroscience. Cogn. Affect. Behav. Neurosci. 4, 564-579.

Bunge S.A., Kahn I., Wallis J.D., Miller E.K., Wagner A.D., 2003. Neural circuits subserving the retrieval and maintenance of abstract rules. J. Neurophysiol. 90, 3419-3428.

Castro L. and Toro M., 2004. The evolution of culture: From primate social learning to human culture. Proc. Natl. Acad. Sci. 101, 10235-10240.

Cavalli-Sforza L.L and Feldman M.W., 1981. Cultural Transmission and Evolution: A Quantitative Approach. Princeton Univ Press, Princeton.

Corbetta M., Shulman G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201-15.

Crone E.A., Donohue S.E., Honomichl R., Wendelken C., Bunge S.A., 2006. Brain regions mediating flexible rule use during development. J. Neurosci. 26, 11239-11247.

Deiber M.P., Wise S.P., Honda M., Catalan M.J., Grafman J., Hallett M. (1997). Frontal and parietal networks for conditional motor learning: a positron emission tomography study. J. Neurophysiol. 78, 977-91.

Deiber M.P., Ibanez V., Honda M., Sadato N., Raman R., Hallett M., 1998. Cerebral processes related to visuomotor imagery and generation of simple finger movements studied with positron emission tomography. NeuroImage 7, 73-85.

Eliassen J.C., Souza T., Sanes J.N., 2003. Experience-dependent activation patterns in human brain during visual-motor associative learning. J. Neurosci. 23,10540-7.

Frey S.H., Gerry V.E., 2006. Modulation of neural activity during observational learning of actions and their sequential orders. J. Neurosci. 26, 13194-13201.

Gazzola V., Rizzolatti G., Wicker B., Keysers C., 2007. The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. NeuroImage 35, 1674-1684.

Gazzola V., Aziz-Zadeh L., Keysers C., 2006. Empathy and the somatotopic auditory mirror system in humans. Curr. Biol. 16, 1824-1829.

Gallese V., Goldman A., 1998. Mirror neurons and the simulation theory of mind-reading. Trends Cogn. Sci. 2, 493-501.

Grèzes J., Armony J.L., Rowe J., Passingham R.E., 2003. Activations related to "mirror" and "canonical" neurons in the human brain: an fMRI study. NeuroImage 18, 928-937.

Hadj-Bouziane F., Boussaoud D., 2003. Neuronal activity in the monkey striatum during conditional visuomotor learning. Exp. Brain Res. 153, 190-6.

Hopfinger J.B., Buonocore M.H., Mangun G.R., 2000. The neural mechanisms of top-down attentional control. Nat Neurosci. 3, 284-91.

Iacoboni M., Molnar-Szakacs I., Gallese V., Buccino G., Mazziotta J.C., Rizzolatti G., 2005. Grasping the intentions of others with one's own mirror neuron system. PLoS Biol. 3, 529-535.

Jeannerod M., 2001. Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. NeuroImage 14, 103-109.

Jensen O., Kaiser J., Lachaux J.P., 2007. Human gamma-frequency oscillations associated with attention and memory. Trends Neurosci. 30, 317–324.

Keysers C., Wicker B., Gazzola V., Anton J.L., Fogassi L., Gallese V., 2004. A touching sight: SII/PV activation during the observation and experience of touch. Neuron 42, 335-46.

Law J.R., Flanery M.A., Wirth S., Yanike M., Smith A.C., Frank L.M., Suzuki W.A., Brown E.N., Stark C.E., 2005. Functional magnetic resonance imaging activity during the gradual acquisition and expression of paired-associate memory. J. Neurosci. 25, 5720-5729.

Molnar-Szakacs I., Iacoboni M., Koski L., Mazziotta J.C., 2005. Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. Cereb. Cortex 7, 986-994.

Molnar-Szakacs I., Kaplan J., Greenfield P.M., Iacoboni M., 2006. Observing complex action sequences: The role of the fronto-parietal mirror neuron system. NeuroImage 33, 923-935.

Nieuwenhuis I.L., Takashima A., Oostenveld R., Fernández G., Jensen O., 2008. Visual areas become less engaged in associative recall following memory stabilization. Neuroimage 40, 1319-27.

Rizzolatti G., Craighero L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169-92.

Rizzolatti G., Fogassi L., Gallese V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2, 661-670.

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

Singer T., Seymour B., O'Doherty J., Kaube H., Dolan R.J., Frith C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. Science 303, 1157-62.

Supèr H., Spekreijse H., Lamme V.A., 2001. A neural correlate of working memory in the monkey primary visual cortex. Science 293, 120-4.

Toni I., Passingham R.E., 1999. Prefrontal-basal ganglia pathways are involved in the learning of arbitrary visuomotor associations : a PET study. Exp. Brain. Res. 127, 19-32.

Toni I., Ramnani N., Josephs O., Ashburner J., Passingham R.E. 2001. Learning arbitrary visuomotor associations: temporal dynamic of brain activity. Neuroimage 14, 1048-1057.

Vidyasagar T.R., Pigarev I.N., 2007. Modulation of neuronal responses in macaque primary visual cortex in a memory task. Eur. J. Neurosci. 25, 2547-57.

Wicker B., Perrett D.I., Baron-Cohen S., Decety J., 2003a. Being the target of another's emotion: a PET study. Neuropsychologia 41, 139-46.

Wicker B., Keysers C., Plailly J., Royet J.P., Gallese V., Rizzolatti G., 2003b. Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. Neuron 40, 655-64.

Wise S.P., di Pellegrino G., Boussaoud D. 1996. The premotor cortex and non-standard sensorimotor mapping. Can. J. Physiol. Pharmacol. 74, 469-482.

Wise S.P., Murray E.A. 2000. Arbitrary associations between antecedents and actions. Trends Neurosci. 23, 271-6.