Is the human Mirror System located within Broca’s area? A selective meta-analysis of fMRI studies of action observation and execution

Pascal Molenberghs
Mirror Neurons


Language within our grasp
Giacomo Rizzolatti and Michael A. Arbib

In monkeys, the rostral part of ventral premotor cortex (area F5) contains neurons that discharge, both when the monkey grasps or manipulates objects and when it observes the experimenter making similar actions. These neurons (mirror neurons) appear to represent a system that matches observed events to similar, internally generated actions, and in this way forms a link between the observer and the actor. Transcranial magnetic stimulation and positron emission tomography (PET) experiments suggest that a mirror system for gesture recognition also exists in humans and includes Broca's area. We propose here that such an observation/execution matching system provides a necessary bridge from 'doing' to 'communicating', as the link between actor and observer becomes a link between the sender and the receiver of each message.


Expanding the mirror: vicarious activity for actions, emotions, and sensations
Christian Keysers and Valeria Gazzola

Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders
Mirriella Dapretto, Mari S Davies, Jennifer H Pfeifer, Ashley A Scott, Marian Sigman, Susan Y Bokshheimer & Marco Iacoboni
“Although doubts have been expressed, most authors share the view that the rostral part of the monkey ventral premotor cortex (area F5) is the monkey homolog of Broca’s area in the human brain.”
Iacoboni et al. (1999). Cortical mechanisms of human imitation. Science
Iacoboni et al. (1999). Cortical mechanisms of human imitation. Science
“We were unable to find evidence of greater activation during imitation than other execution conditions in Broca’s area, even when we reduced the threshold to $p = 0.05$ uncorrected.”

Coordinate-Based Activation Likelihood Estimation (ALE) Meta-Analysis of Neuroimaging Data (Eickhoff et al. 2009, HBM)

What is it?

“Algorithm for coordinate-based meta-analyses which treats reported foci not as points but as spatial probability distributions centered at the given coordinates. ALE maps are then obtained by computing the union of activation probabilities for each voxel. To differentiate true convergence of foci from random clustering (i.e., noise), a permutation test is applied: to obtain an ALE null-distribution the same number of foci as in the real analysis are randomly redistributed throughout the brain and ALE maps are computed as described above. The histogram of the ALE scores obtained from several thousands of random iterations is then used to assign P values to the observed (experimental) values.”
Review

Is the mirror neuron system involved in imitation? A short review and meta-analysis

Pascal Molenberghs *, Ross Cunnington, Jason B. Mattingley

The University of Queensland, Queensland Brain Institute & School of Psychology, St Lucia, Queensland 4072, Australia
Review

Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies

Pascal Molenberghs*, Ross Cunnington, Jason B. Mattingley

The University of Queensland, Queensland Brain Institute & School of Psychology, Queensland 4072, Australia
“One important observation to arise from our findings is that very few of the human fMRI studies (30% of the 76 “classical” mirror studies) included both an “observe” and a corresponding “execute” condition, even though the original single-cell investigations imply that a neuron must respond under both conditions to be considered a mirror neuron.”
What about the 30% of classical studies that did include both action observation and execution condition?
Buccino et al. (2001): Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. European Journal of Neuroscience
A few more interesting observations about mirror neurons ...


Mirror neurons in supplementary motor area, and hippocampus. A subset of these neurons demonstrated excitation during action-execution and inhibition during action-observation. So they are widespread and not all the same.

2) Gallese et al. (1996). Action recognition in the premotor cortex. Brain: Only 17% of neurons in F5 of the macaque had so-called “mirror” properties and they fire less for action observation than for action execution.

3) Kraskov et al. (2009). Neurons within area F5 of the monkey: 29% respond to intransitive actions (no hand-object interaction or apparent goal required to elicit a response during passive observation).

4) Single cell studies in monkeys have also revealed mirror-like properties in the primary motor cortex, dorsal premotor cortex, lateral intraparietal area (LIP) and ventral intraparietal area (Tkach et al., 2007; Dushanova & Donoghue, 2010; Vigneswaran et al., 2013; Shepherd et al. 2009; Ishada et al., 2009)

5) Action perception network seem to be influenced by learning (see e.g., Cecilia Heyes, Emily Cross, ...).
CONCLUSIONS

• Mirror neurons are widespread (including Broca area; e.g., Kilner, 2009) but it seems the majority of the “classical” mirror neurons are located in premotor cortex and inferior + superior parietal lobule rather than Broca area.

• Mirror neurons seem to be somatotopically organized and modality specific

• Mirror Neurons vs Mirror System?

• If the majority of mirror neurons is not located Broca area does this has any implications for its role in language, imitation, action understanding, autism?

• People associate their “brain activity” to easily to the mirror system (e.g., “canonical” neurons).

• Finally, mirror neurons are just a type of multisensory neurons like there are many types of multisensory neurons (e.g., sound/vision). They probably develop and are influenced by associative learning and they are not some “magical” neurons that explain everything about action understanding, imitation, language, autism, ... . All these things are very complex and involve a wide range of brain regions and different types of neurons.
Acknowledgements

Ross Cunnington

Jason Mattingley

Funding:

Australian Government
National Health and Medical Research Council

The University of Queensland
Australia