Imitation Is The Sincerest Form of Flattery

Sarinana, Joshua MIT 2007

Imitation Is The Sincerest Form of Flattery

Image removed due to copyright restrictions.
Photo of a tennis player.

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Monkeys Imitate Too

Images removed due to copyright restrictions.
Photos of George W. Bush and chimpanzees wearing similar expressions.

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Coupling Observation of an action with the Execution of an action

The Mirror Neuron System

Sarinana, Joshua MIT 2007

Requisites for Observational Learning

- Watch/Listen to human or human like action
- Integrate what was watched/listened to with motor preparation
- Execute the action from the learning episode
- Place yourself in the position of the observed*

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Overview

- Anatomy and Physiology of Monkey Mirror Neuron System
- What Else Do Mirror Neurons Encode?
- Homologies in the Human Mirror Neuron System
- Language, Empathy and Autism

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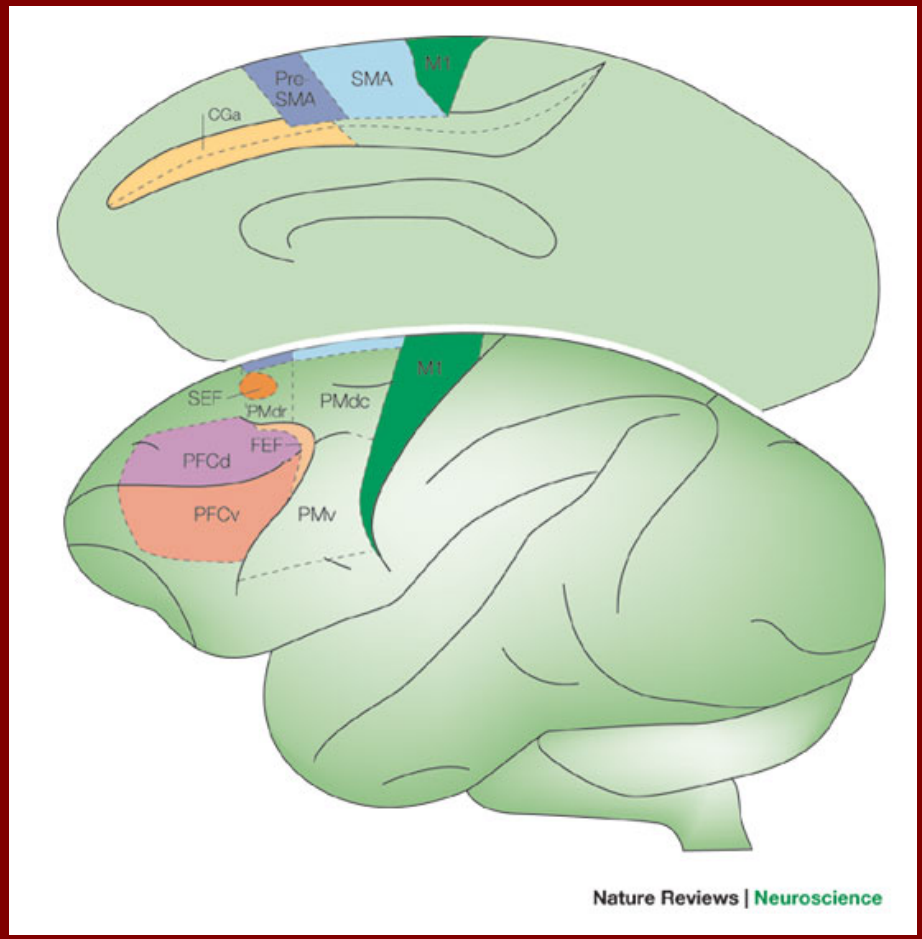
Monkey Cortex



Source: Fig. 6 in Nieder, Andreas. "Counting on Neurons: the Neurobiology of Numerical Competence." *Nature Reviews Neuroscience* 6 (2005): 177-190. Courtesy of the author. Used with permission.

Parietal and Prefrontal Dependent Motor Areas

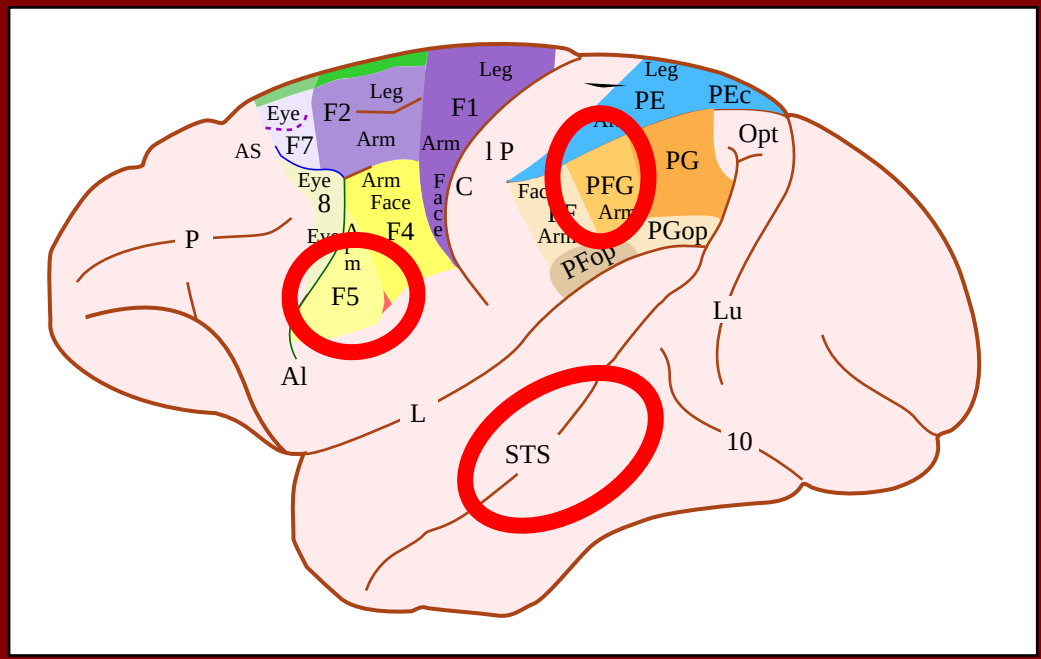


Figure by MIT OpenCourseWare.

The Mirror Neuron System

Sarinana, Joshua MIT 2007

Rizzolatti & Mitelli Electroencephalogr Clin Neurophysiol. 1998

Macaque Cortical Layers

Image removed due to copyright restrictions.
Diagram of different cell layers in cortex, with the granular layer crossed out.
See fifth image down at http://www.benbest.com/science/anatmind/anatmd5.html for base image.

Premotor areas (such as F5) lack the granular layer “agranular”

Sarinana, Joshua MIT 2007

Macaque Cortical Layers

Image removed due to copyright restrictions.
Diagram of different cell layers in cortex (with granular layer retained).
See fifth image down at http://www.benbest.com/science/anatmind/anatmd5.html.

Sensory cortical areas (such as PF and STS) have a very thick granular layer

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Macaque Cortical Layers

Image removed due to copyright restrictions.
Diagram of different cell layers in cortex, with external pyramidal layer highlighted.
See fifth image down at http://www.benbest.com/science/anatmind/anatmd5.html.

Receives input from other cortical areas

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Ventral Premotor Cortex (Area F5)

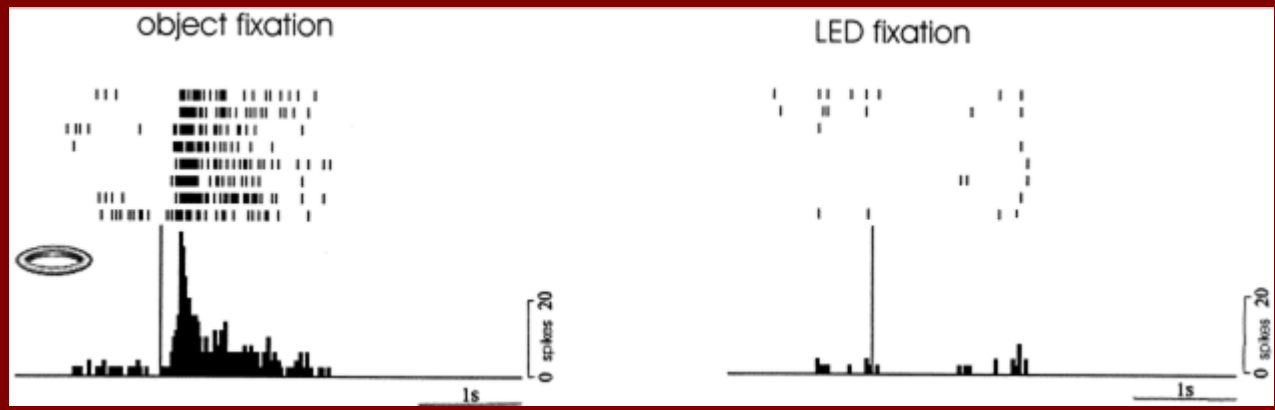
Multimodal cell activity

- Active during object fixation
- Active during observation of certain actions
- Active during action execution
- Stimulation of F5 results in hand and mouth movements
- Homologous to Broca's Area

Sarinana, Joshua MIT 2007

Two Neuron Types In F5

Canonical Neurons



These cells only fire during object fixation **(visual input)** and are not mirror neurons

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Rizzolatti & Luppino Neuron 2001

F5 Mirror Neurons

Active during observation of an action AND Active during imitation of observed action

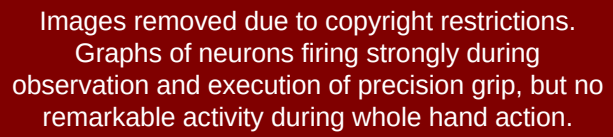
Image removed due to copyright restrictions.

See figure 1a in Rizzolatti, Giacomo, Leonardo Fogassi & Vittorio Gallese.
“Neurophysiological Mechanisms Underlying the Understanding and Imitation of Action.”
Nature Reviews Neuroscience 2 (2001): 661-670.

F5 Mirror Neurons

Active during observation of an action AND Active during imitation of observed action

Monkey observes precision grip



Monkey gives precision grip action

Monkey gives whole hand action

Rizzolatti et al Nat. Rev. Neurosci. 2001

If F5 is a premotor area why does it respond to visual stimuli?

What information is F5 receiving?

Inferior Parietal Lobule (Area PF)

Contains Area **PF**

Projects to The Ventral Premotor Cortex (**F5**)

Integration Site of Visual and Motor Sensory Information (Visuo-Motor Area)

Contains Mirror Neurons

F5 Receives Input From the **Inferior Parietal Lobule (PF)**

Image removed due to copyright restrictions.
Illustration of F5 and PF areas in monkey brain.

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Rizzolatti & Mitelli Electroencephalogr Clin Neurophysiol. 1998

F5 Receives Input From Area **PF**

PF Neurons Display Mirror Neuron Qualities

Image removed due to copyright restrictions.
Graphs showing neuronal responses by PF neurons to motor and visual activities, which are similar to those seen in mirror neurons.

This image was originally parts of figure 1 in Fogassi, et al. "Parietal Lobe: From Action Organization to Intention Understanding." *Science* 308 (2005): 662 – 667.

Sarinana, Joshua MIT 2007

Fogassi et al Science 2005

Superior Temporal Sulcus (STS)

Processes High Order Visual Stimuli

Projects to Posterior Parietal Cortex (PF)

Sends Processed Visual Information

Does not have Mirror Like Neurons

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Superior Temporal Sulcus (STS)

Image removed due to copyright restrictions.
Graph of neuronal responses in the STS: high levels of activity observed when viewing actions such as hand with food approaching mouth, or head/mouth moving in the direction of a hand holding food, but the responses were much lower while viewing an empty hand moving towards a mouth, or a hand with food moving towards nothing in particular.

Fires During the **Observation** of goal-directed actions

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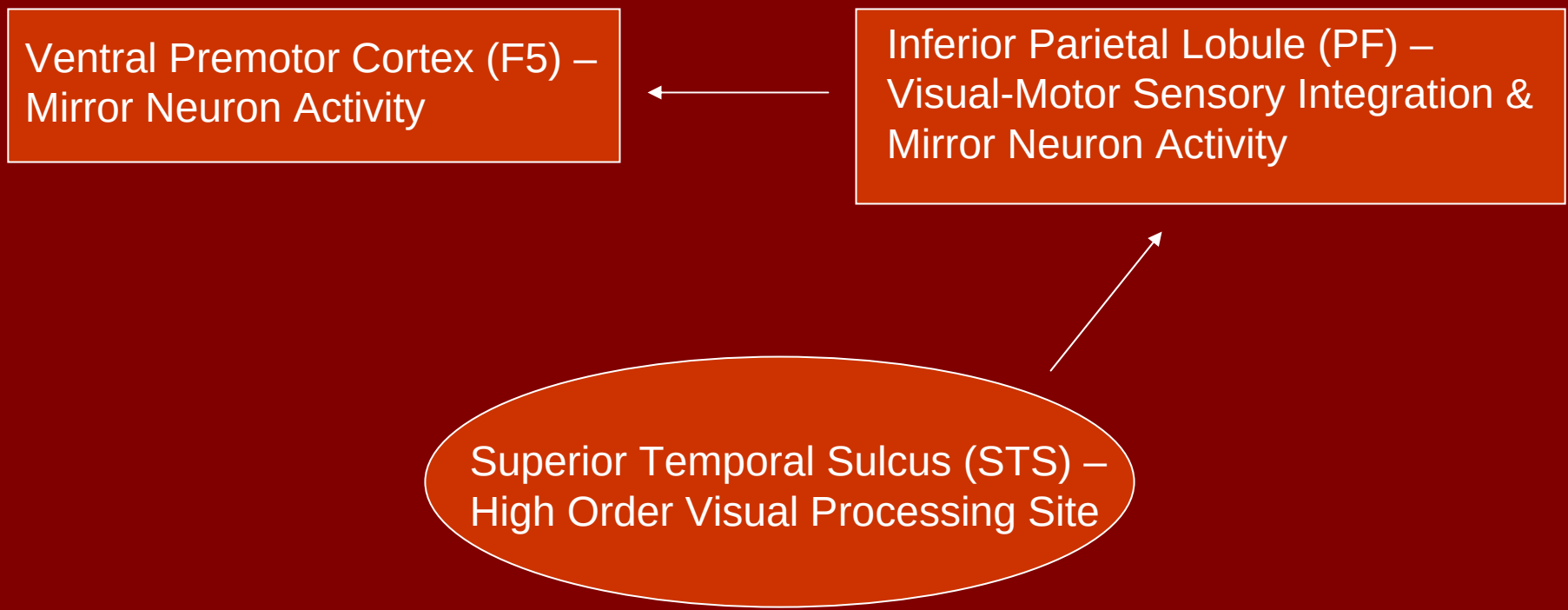
Minimal Mirror Neuron System Architecture



Sarinana, Joshua MIT 2007

Conclusions

- The mirror neuron system consists of areas: F5, PF and STS
- STS Projects to PF and PF projects to F5
- F5 is Agranular while PF and STS have a thick granular layer
- Cortical areas communicate via Layer III Pyramidal Neurons
- Both Areas F5 and PF contain mirror Neurons (Layer III Pyramidal Neurons)
- Area PF integrates visual and motor sensory information
- The STS does not contain mirror neurons but encodes visual actions
- Mirror neurons must be active during **both**:
  - Observed **AND** Executed Actions

Sarinana, Joshua MIT 2007

Overview

- Anatomy and Physiology of Macaque Cortex
- What Do Mirror Neurons Encode Exactly?
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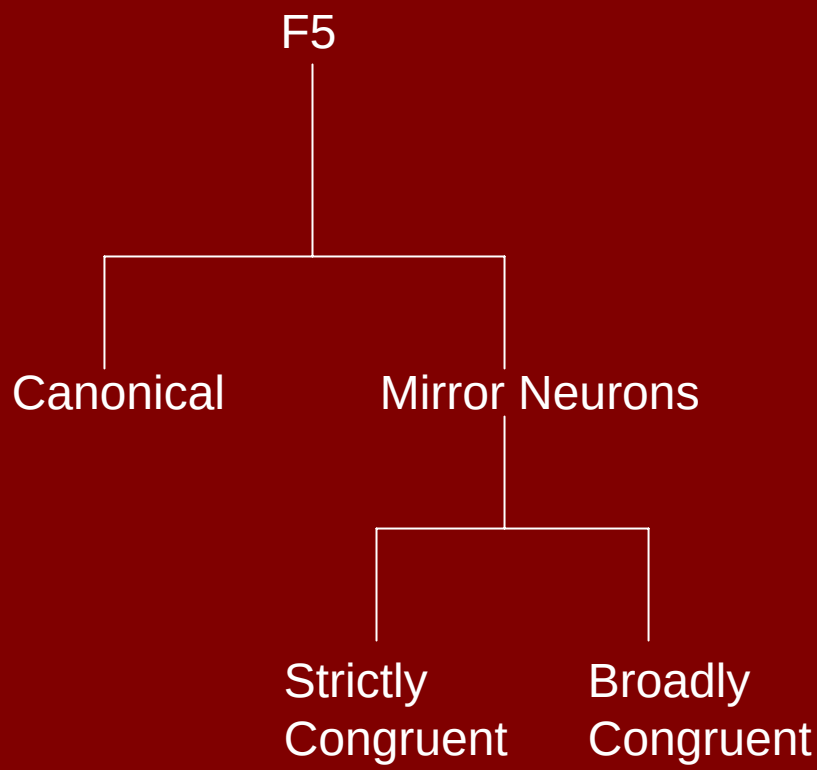
Two Types of **F5** Mirror Neurons



Sarinana, Joshua MIT 2007

Two Types of **F5** Mirror Neurons

Strictly Congruent Mirror Neurons

Line demarks Experimenter Touching food

Line demarks Opening of the Testing Box

Images removed due to copyright restrictions.

Graphs of neurons firing strongly during observation and execution of precision grip, but no remarkable activity during whole hand action. Neuronal spikes occur right around placement of the line in the first graph; spikes occur shortly after the line in the second graph.

See Fig. 9 in Gallese, Vittorio et al. "Action recognition in the premotor cortex." *Brain* 119 (1996): 593-609.

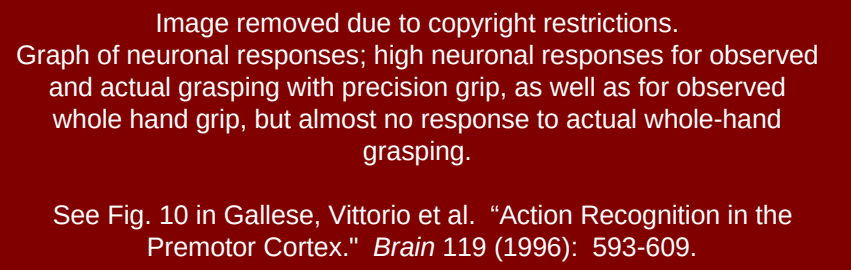
Monkey observes precision grip

Monkey gives precision grip action

Monkey gives whole hand action

Broadly Congruent Mirror Neurons

Observed grasping with precision grip Observed with whole hand



Monkey grasps with precision grip Monkey grasps with whole hand

Mirror Neurons

Strictly congruent

- Observed motor actions and goals = executed motor actions and goals
- Similar to true imitation
- ~1/3 of F5 mirror neurons

Broadly Congruent

- Observed actions do not fully match their imitated action
- Similar to emulation
- ~2/3 of F5 mirror neurons

Mirror Neurons Require Goal Related Actions

Line demarks touching food

Images removed due to copyright restrictions.
Graphs of experimental results, showing that in order to elicit a response from mirror neurons, experimenter had to be touching food, not just an empty board.

See Fig. 4a and 4b in Gallese, Vittorio et al. "Action Recognition in the Premotor Cortex." *Brain* 119 (1996): 593-609.

F5 Auditory Mirror Neurons

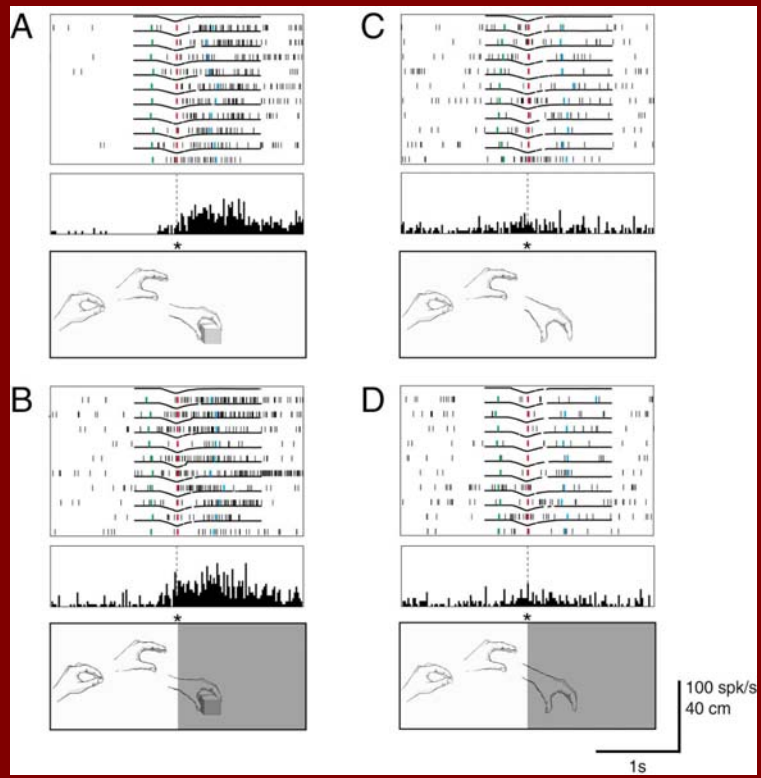
Images removed due to copyright restrictions.

See Fig. 2 in Kohler, Evelyne et al. "Hearing Sounds, Understanding Actions: Action Representation in Mirror Neurons." *Science* 297 (2002): 846 – 848.

Visual representation is not necessary in some F5 mirror neurons

Auditory representation is sufficient in some F5 mirror neurons

Mirror Neurons Encode Intention



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Umilta Neuron 2001

Conclusions

- F5 encodes for the goal and intention of executed actions
- F5 encodes auditory information
  - visual input is not necessary for F5 activity
- PF encodes for visuo-motor activity
- STS encodes for description of observed action

Do Monkeys Really Imitate?

- Imitative abilities of monkeys are limited
- In studies monkeys observe then execute
- Does imitation require execution of observed action during observation
- Monkey mirror neuron system may have allowed monkeys to be “Imitation-Ready”

Sarinana, Joshua MIT 2007

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Human Mirror Neuron System

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Human Mirror Neuron System Core

- Inferior Frontal Gyrus (IFG)
- Posterior Parietal Cortex (PPC)
- Superior Temporal Sulcus (STS)

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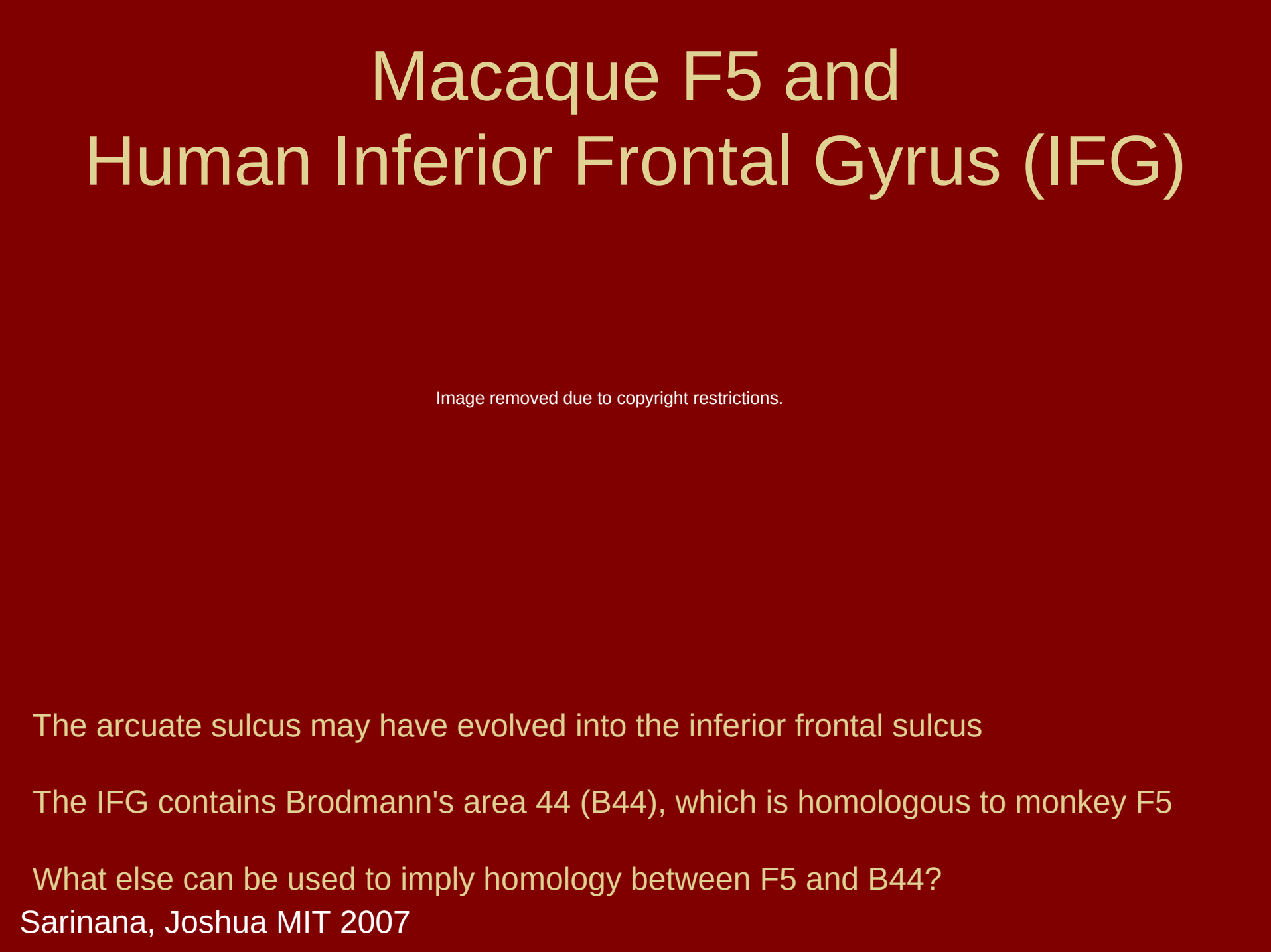
Macaque F5 and Human Inferior Frontal Gyrus (IFG)

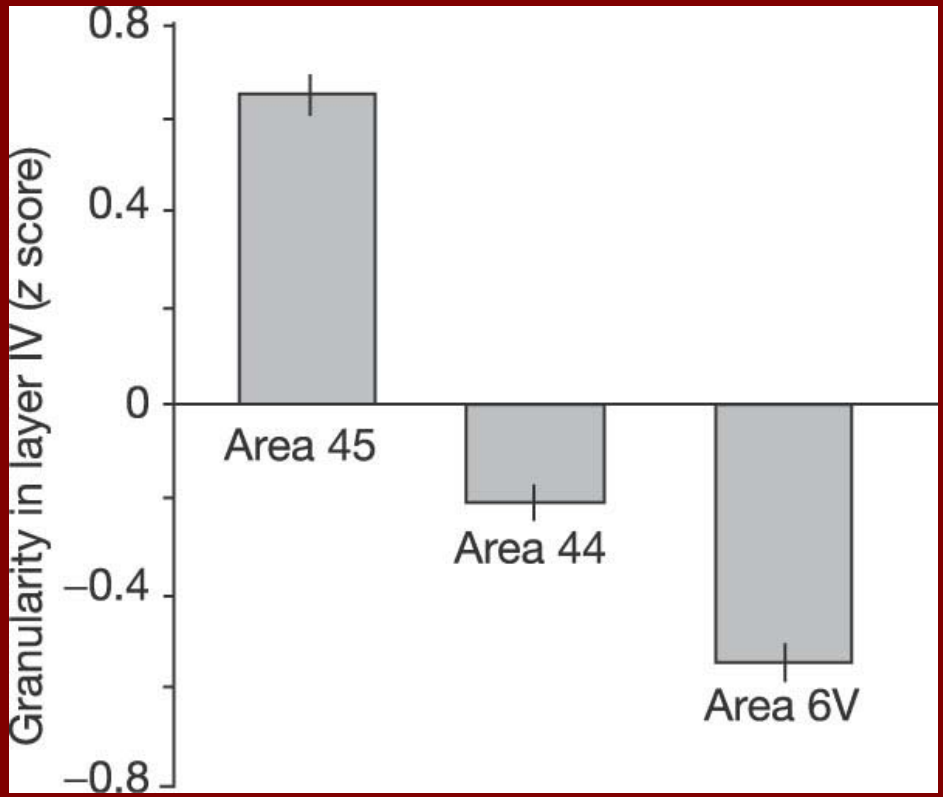


The arcuate sulcus may have evolved into the inferior frontal sulcus

The IFG contains Brodmann's area 44 (B44), which is homologous to monkey F5

What else can be used to imply homology between F5 and B44?

Granularity of Area 44



B44 has less granular cells, but not to the extent of the agranular region of F5

Sarinana, Joshua MIT 2007

Human Mirror Neuron Activity

Image removed due to copyright restrictions.
See Fig. 1 in Iacoboni, Marco et al. "Cortical Mechanisms of Human Imitation." *Science* 24 (1999): 2526-2528.

Sarinana, Joshua MIT 2007

Iacoboni et al Science 1999

B44 Mirror Neuron Activity

Image removed due to copyright restrictions.
See Fig. 2 in Iacoboni, Marco et al. "Cortical Mechanisms of Human Imitation." *Science* 24 (1999): 2526-2528.

Sarinana, Joshua MIT 2007

Iacoboni et al Science 1999

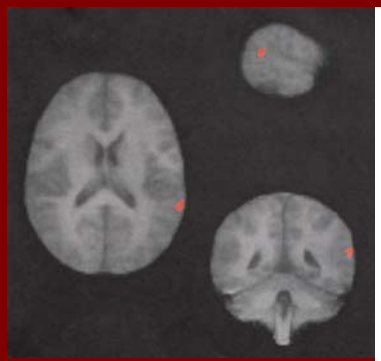
Posterior Parietal Cortex Mirror Neuron Activity (Homologous to PF)

Image removed due to copyright restrictions.
See Fig. 2 in Iacoboni, Marco et al. "Cortical Mechanisms of Human Imitation." *Science* 24 (1999): 2526-2528.

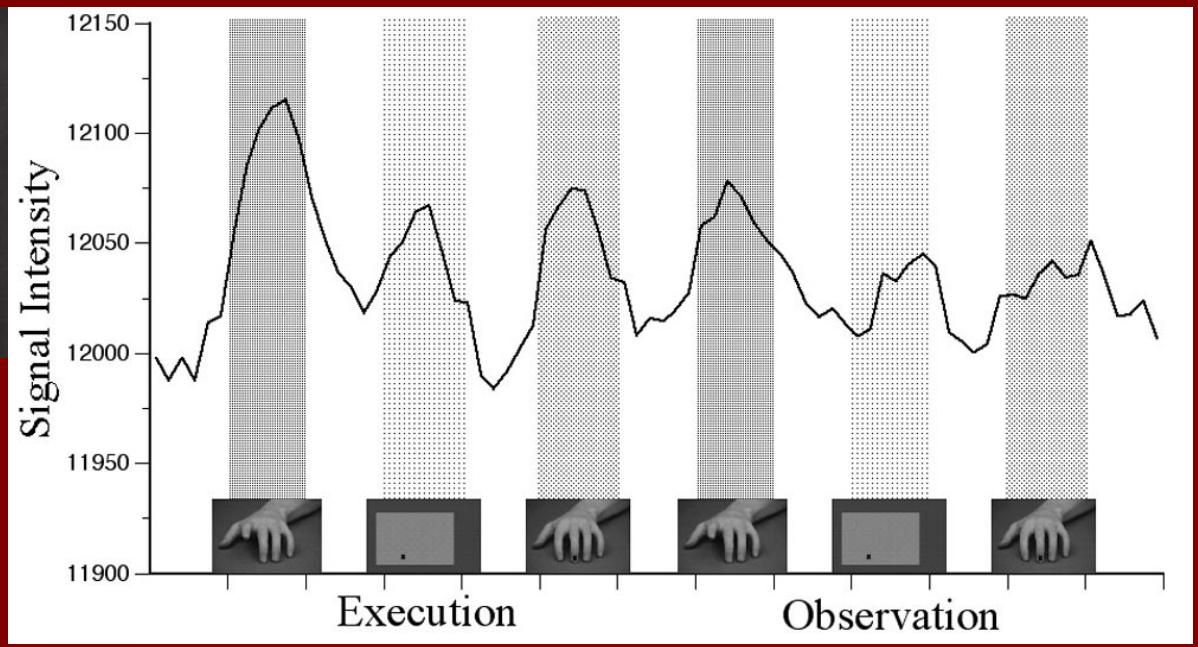
Sarinana, Joshua MIT 2007

Iacoboni et al Science 1999

Does The Human Superior Temporal Sulcus (STS) Have Mirror Neurons?



STS



Sarinana, Joshua MIT 2007

Iacoboni et al PNAS 2001

STS Mirror Neuron Like Activity

- Monkeys do not show STS mirror neuron activity
- Humans seemingly do
- Why should this be the case?

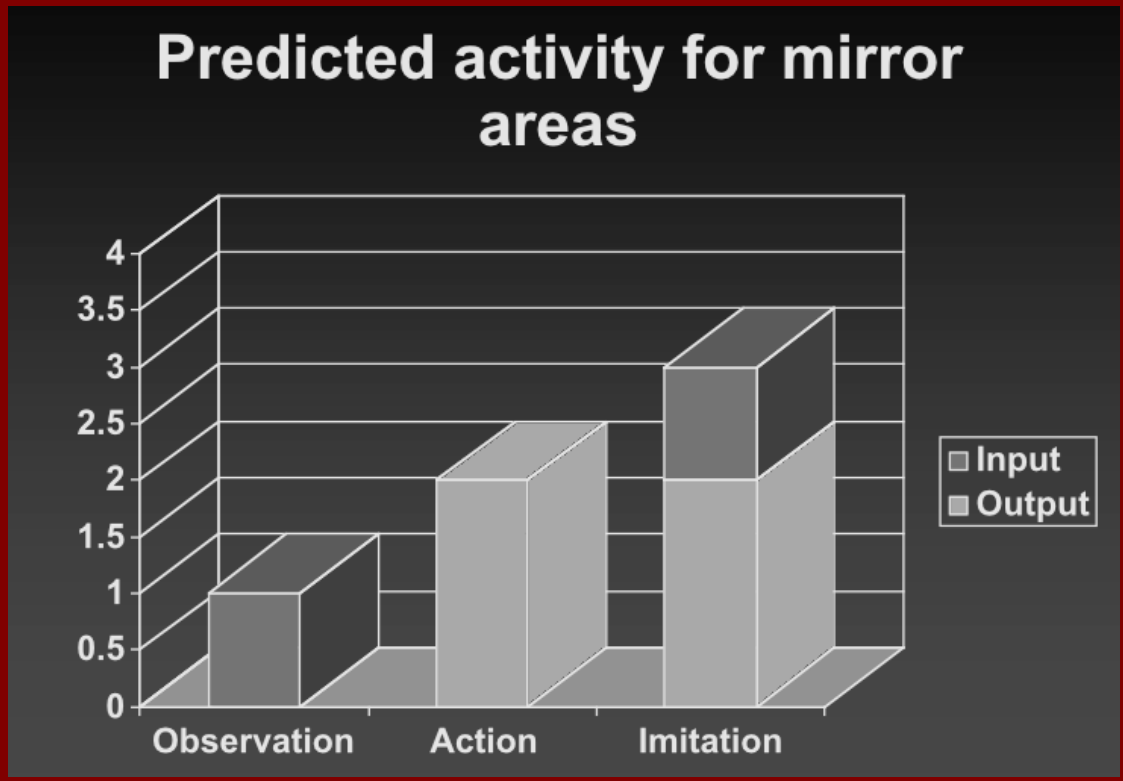
Direct Matching Hypothesis

"Imitation may be based on a mechanism directly matching the observed action onto an internal motor representation of that action"

Sarinana, Joshua MIT 2007

Iacoboni et al Science 1999

Direct Matching Hypothesis Predictions



Human & Monkey

Human

Figure from Iacoboni, M. "Understanding others: imitation, language, empathy." In *Perspectives on Imitation: From Cognitive Neuroscience to Social Science*. Edited by S. Hurley and N. Chater. Courtesy of MIT Press. Used with permission.

Dorsal vs. Ventral B44

Image removed due to copyright restrictions.
fMRI images showing locations of B44 areas.

See Fig. 1 in Molnar-Szakacs, Istvan, et al. "Functional Segregation within Pars Opercularis of the Inferior Frontal Gyrus: Evidence from fMRI Studies of Imitation and Action Observation." *Cerebral Cortex* 15 (2005): 986-994.

Sarinana, Joshua MIT 2007

Istvan Molnar-Szakacs Cerebral Cortex 2004

Dorsal vs. Ventral B44

Dorsal B44
- Exhibits mirror neuron activity

Images removed due to copyright restrictions.
Bar graphs showing mirror neuron activity, or lack thereof, in B44 areas.

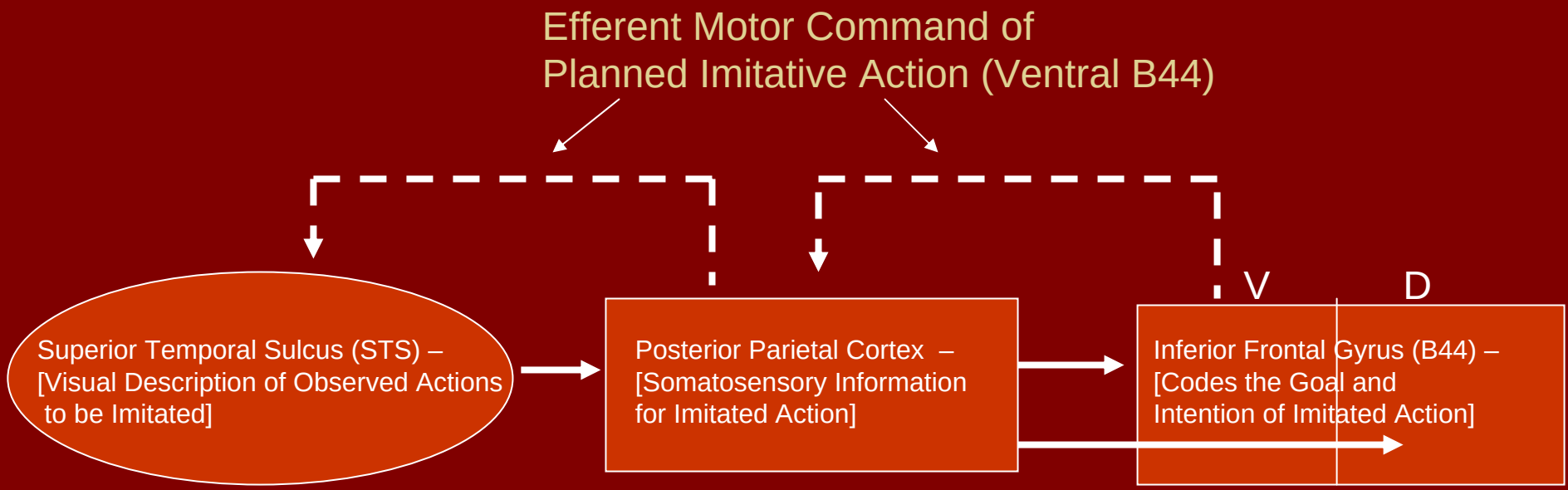
See figures 3 and 4 in Molnar-Szakacs, Istvan, et al. "Functional Segregation within Pars Opercularis of the Inferior Frontal Gyrus: Evidence from fMRI Studies of Imitation and Action Observation." *Cerebral Cortex* 15 (2005): 986-994.

Ventral B44
- No mirror neuron activity
- Only active during imitation

Sarinana, Joshua MIT 2007

Istvan Molnar-Szakacs Cerebral Cortex 2004

The Predictive Hypothesis



If there is a “match” between the efferent copy from vB44 with the STS description of that action then the action is Imitated

If there is an error (no matching) between vB44 and STS then the motor plan is corrected until a match is reached

Sarinana, Joshua MIT 2007

Homologous Structure Review

- Brodmann's Area 44 (B44) is homologous to monkey Area F5
- Posterior Parietal Cortex (PPC) is homologous to monkey Area PF
- Superior Temporal Sulcus (STS) both in humans and monkeys

Conclusions

- B44 and PPC contain mirror neurons
  - dorsal B44 contains mirror neurons while ventral B44 does not
- The STS does not have mirror neurons but receives efferent imitative predictions from B44
- The predictive hypothesis explains the F5 visual response and STS activity*

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Broca’s Area and Imitation

Images removed due to copyright restrictions.
Images from imitation experiment of a finger pressing a key on a keyboard, and brain scan images with dots marking the left and right pars opercularis, as well as a representative target location for occipital site.

See figures 1 and 2 in Heiser, et al. “The Essential Role of Broca's Area in Imitation." *European Journal of Neuroscience* 17 (2003): 1123-1128.

Transcranial Magnetic Stimulation (TMS) to inactivate IFG

Heiser et al Eur JNeurosci. 2003

Broca's Area and Imitation

Image removed due to copyright restrictions.
See figure 3 in Heiser, et al. "The essential Role of Broca's Area in Imitation."
European Journal of Neuroscience 17 (2003): 1123-1128.

Implicates Broca's Area in **imitation**

Monkey studies show that sound also activates mirror neurons

Because Broca's area is important in language and mirror neurons have auditory access, mirror neurons may be Important in speech perception

Sarinana, Joshua MIT 2007

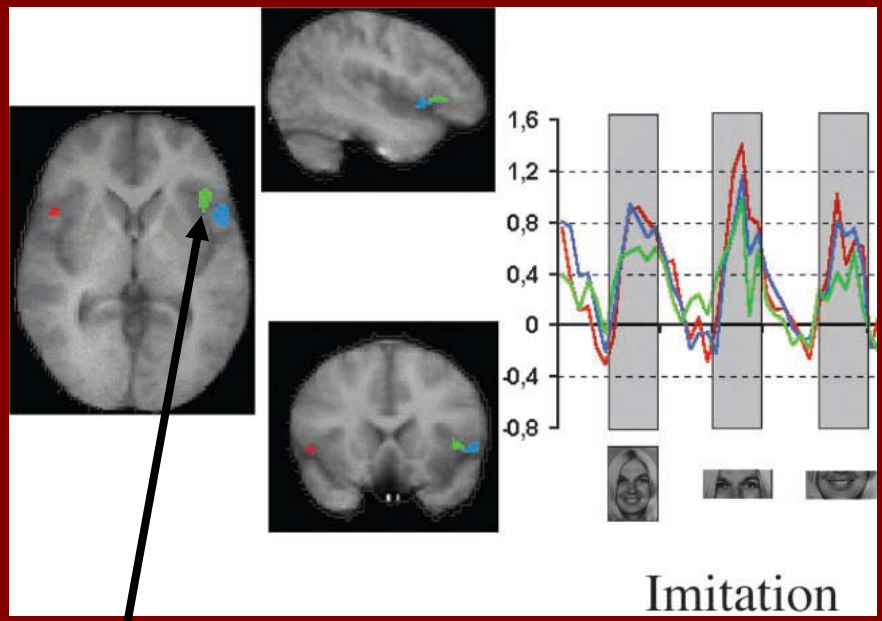
Heiser et al Eur JNeurosci. 2003

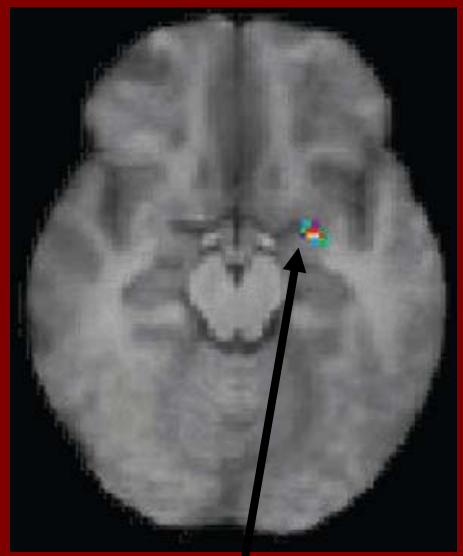
Empathy

- Empathy requires understanding others situations, which may require imitative abilities
- Insular cortex connects to limbic system and with posterior parietal cortex, inferior frontal cortex and the superior temporal sulcus (STS)
- Insula may relay information between these structures

Sarinana, Joshua MIT 2007

Empathy





Right Insula

Amygdala

Sarinana, Joshua MIT 2007

Carr et al PNAS 2003

Autism Spectrum Disorder (ASD)

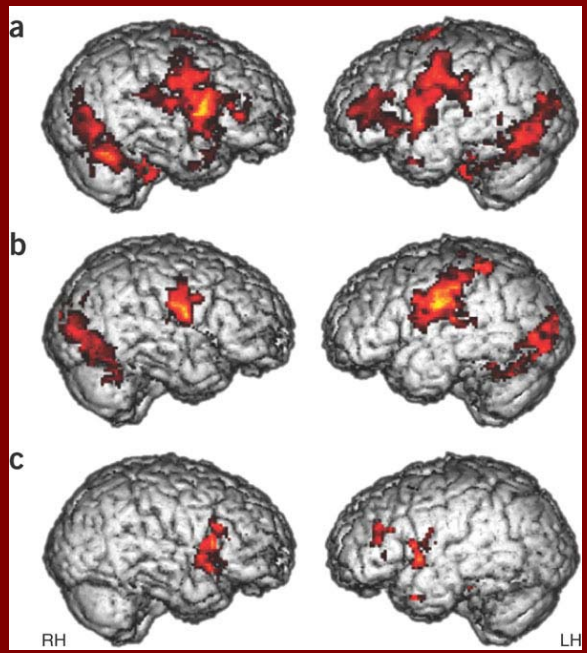
- Those with ASD have deficits in imitation, language and empathy
- Do those with ASD have altered IFG activity?

Autism Spectrum Disorder (ASD)

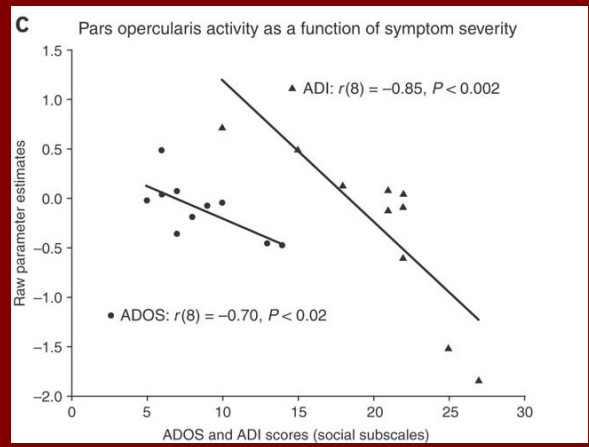
Control

ASD

Difference



Observation



B44 Activity vs. ASD Diagnostic

Source: Figures 1 and 3c from Dapretto, Mirella, et al. "Understanding Emotions in Others: Mirror Neuron Dysfunction in Children with Autism Spectrum Disorders." *Nature Neuroscience* 9 (2005): 28-30. Courtesy of the authors. Used with permission.

Sarinana, Joshua MIT 2007

Dapretto et al Nat. Neurosci. 2006

Do MIT Students Have Mirror Neurons

Sarinana, Joshua MIT 2007