Eight Problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans

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Introduction

- Motor Theories of Cognition
  - In his *Essay Towards a New Theory of Vision* (1709) Berkeley uses a motor representation to describe depth perception.
  - Motor theory in Movement and Mental Imagery (1916) by Margeret Floy Washburn explains consciousness as a phenomena arising from excitation and inhibition of motor discharge.
  - "According to my view, thought processes are really motor habits in the larynx" (Watson, 1913)
  - Motor theory of speech perception-motor movement not only needed for production of speech but also for perception

Introduction (cont.)

- The range of abilities and disorders to which the mirror neuron theory has been extended includes speech perception, music perception, empathy, altruism, emotion, theory of mind, imitation, autism spectrum disorder, among others.

Mirror Neurons: The Data

- F5 cells:
  - mirror neurons comprised 17% of sampled cells
  - Roughly half (55%) were selective for one type of action
  - The cells did not respond to visually presented objects or food items, faces, non-goal-directed body movements, goal-directed actions made using tools, mimicking of grasping in the absence of an object (pantomime), or gestures having emotional meaning
  - The perception of a graspable object is sufficient to trigger the activation of cells in motor area F5

Mirror Neurons: The Theory

- How do we define action understanding?
  - the capacity to recognize that an individual is performing an action, to differentiate this action from others analogous to it, and to use this information in order to act appropriately" Gallese et al. (1996)
  - Problems:
    - an individual could produce meaningless, non-goal-directed actions (e.g., flailing the arms, which should yield no mirror neuron activity), yet the action could still be recognized, differentiated from similar ones and reacted upon appropriately.

Mirror Neurons: The Theory (Cont.)

- How do we define action understanding?
  - "the capacity to achieve the internal description of an action and to use it to organize appropriate future behaviour" Rizzolatti et al. (2001)
  - Problems:
    - How do you define internal description?

Mirror Neurons: The Theory (Cont.)

- How do we define action understanding?
  - "Each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's premotor cortex. This automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual. Thus, the mirror system transforms visual information into knowledge" Rizzolatti and Craighero (2004)
  - Problems:
    - the idea that understanding is achieved by knowing the "outcome" is also somewhat vague because "outcome" is not defined.

Mirror Neurons: The Theory (Cont.)

- How do we define action understanding?
  - "A mere visual representation [of an action], without involvement of the motor system, provides a description of the visible aspects of the movement of the agent, but does not give information critical for understanding action semantics, i.e., what the action is about, what its goal is, and how it is related to other actions" Nelissen et al. (2005)
  - Problems:
    - What is the action of grasping a peanut "about"? What is the "goal" of such an action? And on what level of analysis is "relation" between actions defined?

Mirror Neurons: The Theory (Cont.)

- Basis for applying it to humans:
  - (i) the fact that pantomime recognition deficits exist in aphasia (Gainotti & Lemmo, 1976).
  - (ii) a PET study in humans showing activation in Broca's region during action observation (Rizzolatti et al., 1996).
  - (iii) a trans- cranial magnetic stimulation (TMS) study that showed enhanced distal muscle motor-evoked potentials (MEPs) during action observation (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995).

Mirror Neurons: The Theory (Cont.)

- Why it doesn't work:
  - i) Mirror neurons do not respond to pantomimed actions and so pantomime recognition should not rely on the mirror system. Further, pantomime recognition deficits were not associated with frontal lesions, but rather were predominantly associated with posterior lesions (Heilman, Rothi, & Valenstein, 1982).
  - (ii) The PET study showing Broca's region activation during action observation failed to show overlapping activation during grasping production (Rizzolatti et al., 1996), in contrast to the central mirror neuron observation.
  - (iii) the TMS finding of peripheral motor activation during action observation directly contradicted the early demonstration in monkeys that M1 and the peripheral motor system did not exhibit mirror properties (Gallese et al., 1996)

There Is No Evidence in Monkeys That Mirror Neurons Support Action Understanding

- The mirror neuron theory of action understanding predicts that disruption of motor areas in F5 should produce deficits in action perception, although in macaques it has only shown disruption in grasping.
- Rizzolatti and Craighero say this cannot be studied because the mirror system
  - MNS is bilateral and involves parietal structures
  - There are other mechanisms that control action recognition
  - If an entire mirror system were lesioned it would be too difficult to analyze given that more general cognitive deficits would result.

There Is No Evidence in Monkeys That Mirror Neurons Support Action Understanding (Cont.)

- The rebuttal to this criticism is that if motor systems do indeed underlie action understanding, then disrupting motor systems in F5 would equally impair action understanding just as much as it would impair other motor behavior.
- If motor behavior and action understanding appear independent with F5 disruption, then it would be evidence that motor systems do not have a significant role in action understanding.

There Is No Evidence in Monkeys That Mirror Neurons Support Action Understanding (Cont.)

- Experiment #1
  - 15% of mirror neurons respond to action associated sounds when presented in isolation
    - If action understanding is controlled by mirror neurons then it should entail the meaning of the observed action not just the visual features.
  - Kohler found that 85% do not involve the meaning, but the other 15% of audiovisual mirror neurons may just be associated with the F5 area without having any real significance.

There Is No Evidence in Monkeys That Mirror Neurons Support Action Understanding (Cont.)

- Experiment #2
  - Monkeys will respond to a hidden action if they know that the object is behind the screen
    - This suggests that the meaning is the drive behind the response not just the physical object.
  - Half of the mirror neurons still did not code action meaning

There Is No Evidence in Monkeys That Mirror Neurons Support Action Understanding (Cont.)

- Experiment #3
  - Inferior Parietal Lobule
    - Monkeys had to grasp food to put in mouth or grasp object to put in container.
    - IPL cells responded to the goal of that action, even when the placing action stopped in close proximity to the mouth and involved grasping a piece of food.
    - In perception and action, IPL cells are selective for the specific goal rather than the sensory motor features of an action.

Action Understanding Can Be Achieved via Nonmirror Neuron Mechanisms

- Rizzolati and Craighero noted in 2004 that the MNS might not be the only mechanism of action understanding.
  - This is problematic because it associates action understanding with object understanding
    - Object responses in F5 are not the neural basis for, therefore it wouldn't be for action understanding either.
- Object information processed for meaning in the temporal lobe can connect to the motor programs, explaining the object response of F5 cells even though meaning is not coded there.

M1 Contains Mirror Neurons

- Mirror neurons are present in primary motor cortex of macaque monkeys.
- The lack of MN in M1 meant that monkeys were not generating movement responses during the perception of actions
  - This ruled out the possibility that response based on MN were a motor command that triggered higher level cognitive functions

The Relation between Macaque Mirror Neurons and the "Mirror System" in Humans Is Either Nonparallel or Undetermined

- Hickok's Claim:
  - mirror neuron function has been generalized to a wide range of human behaviors
  - much of the excitement over mirror neurons is directly related to their potential to explain complex human capacities and disorders

The Relation between Macaque Mirror Neurons and the "Mirror System" in Humans Is Either Nonparallel or Undetermined

- "Mirror neurons are primarily thought to be involved in perception and comprehension of motor actions, but they may also play a critical role in higher order cognitive processes such as imitation, theory of mind, language, and empathy, all of which are known to be impaired in individuals with autism spectrum disorders" Oberman et al. (2005)

The Relation between Macaque Mirror Neurons and the "Mirror System" in Humans Is Either Nonparallel or Undetermined

- Problem:
  - the species of monkeys studied and that have shown to possess mirror neurons do not, to our knowledge, possess any of these higher-order cognitive processes (imitation, theory of mind, language, and empathy)
  - Other species of monkeys that possesses the higher-order cognitive processes has not been shown conclusively to possess mirror neurons
  - Monkey data and theories are imported to human work without empirical validation of the assumptions

The Relation between Macaque Mirror Neurons and the "Mirror System" in Humans Is Either Nonparallel or Undetermined

- relation between the macaque mirror neuron system and the hypothesized human homologue remains to be clarified
  - If mirror neurons exist in humans as is claimed, the system should be demonstrably different from in the monkey system
  - Therefore it cannot be assumed that monkey data will hold in the human system

The Relation between Macaque Mirror Neurons and the "Mirror System" in Humans Is Either Nonparallel or Undetermined

- Evidence:
  - (Morin & Grezes, 2008) suggested that human BA 44 is not the homologue of the macaque mirror neuron F5 region (object-directed actions)
  - BA 44 does not distinguish between object-directed actions and actions that are non-object directed.
  - Instead, Morin and Grezes (2008) point out that a more posterior region, ventral premotor cortex (BA 6), is activated significantly more often during the perception of object-directed action than actions without object goals

The Relation between Macaque Mirror Neurons and the "Mirror System" in Humans Is Either Nonparallel or Undetermined

- There is nothing wrong with using animal models to generate testable hypotheses in humans—indeed, this is a productive and important research strategy.
- The problem in the case of mirror neurons is that the system has been generalized to humans without systematic validation

Action Understanding in Humans Dissociates from Neurophysiological Indices of the Human "Mirror System"

- Action understanding can occur without activation of known mirror neuron areas:
  - (Buccino et al., 2004) examined functional activations during the perception of biting actions or communicative gestures performed by a human, a monkey, or a dog.
  - Viewing biting actions activated regions thought to be part of the human mirror system, the left IFG and the precentral gyrus for all species
  - Viewing communicative gestures elicited activation of these frontal mirror systems for actions performed by a human (lip-reading) and a monkey (lip smacking), but not a dog (barking)

Action Understanding in Humans Dissociates from Neurophysiological Indices of the Human "Mirror System"

- On the assumption that the study participants "understood" all three communicative actions, the dissociation occurs in that only the human and monkey actions resulted in "mirror system" activation.
  - result clearly shows that actions can be understood without the mirror system
  - mirror system activity is not particularly correlated with action understanding
- we are fully capable of understanding actions we have never produced

Action Understanding and Action Production Dissociate

- There is no evidence that deactivation of the monkey mirror system disrupts action understanding
- The human mirror neuron theory of action understanding holds several predictions to be true:
  - One such prediction is that action understanding and action production should be strongly correlated.
  - these two abilities can be correlated in group studies, and there is strong evidence that they are quite dissociable.

Action Understanding and Action Production Dissociate

- Group study 21 patients with limb apraxia
  - found a correlation ($r \approx .5$) between a gesture discrimination task (judging whether or not an action is performed correctly) and a gesture production task (asking subjects "to perform seven complex actions that required the use of real objects")
  - Study showed that while 14 of the 21 patients with limb apraxia had "a severe gesture recognition deficit," 7 patients "presented with no deficit" indicating that the two abilities are dissociable.

Action Understanding and Action Production Dissociate

- Sign language provides additional evidence for the dissociation between action production and action understanding.
  - For example, Case "Gail D." presented with very severe deficits in sign language production associated with a large left frontal lobe lesion, yet her comprehension of sign language was well-preserved (Poizner, Klima, & Bellugi, 1987).

Damage to the Inferior Frontal Gyrus Is Not Correlated with Action Understanding Deficits

- If BA 44/6 is the homologue of F5
  - the damage in this region would result in understanding deficits
- The evidence doesn't support this prediction

Damage to the Inferior Frontal Gyrus Is Not Correlated with Action Understanding Deficits

- Heilman et al. (1982)
  - Parietal lobe lesions → production & comprehension deficits
  - Frontal lesions → only production deficits

- Discussions:
  - Parietal lobe also contains MN, so, it is consistent with MN claims
  - But, one would have to conclude that portions of MNS in BA 44/6 do not support action understanding
  - Contrary to Rizzolatti et al.'s claims:
    "it is motor representation that underlie action understanding"

Damage to the Inferior Frontal Gyrus Is Not Correlated with Action Understanding Deficits

(Mixed result regarding the anatomical correlate of action understanding deficit)

- Buxbaum et al. (2005)
  - Confirmed earlier observations
  - Showed that lesions to the inferior parietal lobe are associated with object related gesture recognition deficit
- Saygin, Wilson, Dronkers, & Bates (2004)
  - Reported that: lesions to BA 44/6/4 are associated with action comprehension

Damage to the Inferior Frontal Gyrus Is Not Correlated with Action Understanding Deficits

Saygin, Wilson, Dronkers, & Bates (2004)

- Discussion (cont.)
  - (experimental subject)
    - The study uses aphasic patients (not unselected/ patients selected on the basis of gesture-related deficits), which may have biased their findings
  - (method)
    - the study didn't use dynamic actions as stimuli, but static pictures of pantomimed actions (the subject pointed the pictured object that best fit the action).
  - The relation between action understanding in dynamic actions & static actions are unknown
    - the interpretation of this study is further compromised

Damage to the Inferior Frontal Gyrus Is Not Correlated with Action Understanding Deficits

Saygin, Wilson, Dronkers, & Bates (2004)

However, it is relevant that

- deficits in the understanding of linguistically specified actions
  - dissociated behaviorally from understanding of pictured actions
  - were not associated with lesions to BA 44/6/4
  - were associated with portions of the superior temporal gyrus, insula, and inferior parietal lobe.

- one can conclude that what's being mapped in the study & what's associated with BA 44/6/4 isn't "action semantics", as access to this information is available via other routes.

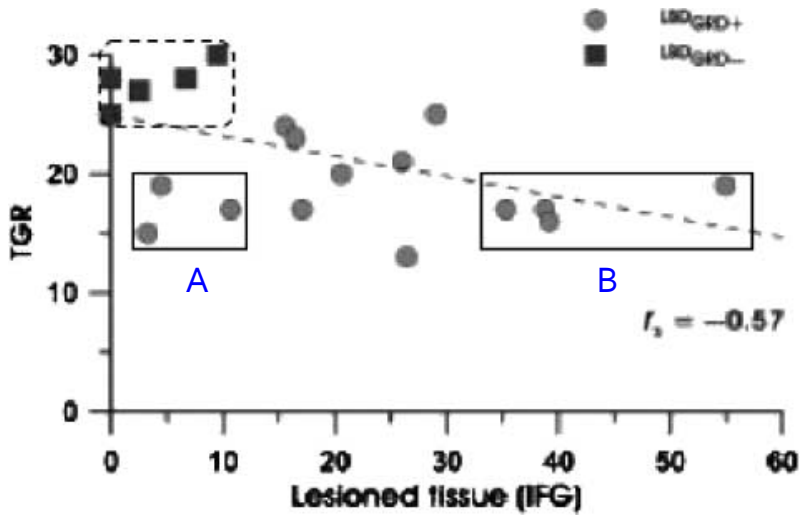
- Thus, this study provides evidence against the view that the meaning of actions is encoded in motor representations in motor cortex.

Damage to the Inferior Frontal Gyrus Is Not Correlated with Action Understanding Deficits

- Pazzaglia et al. (2008)
  - (method)
    - they compare lesions in patients with limb apraxia, with & without gesture discrimination deficits
  - (result)
    - subtraction of the lesions in these 2 groups of patients identified that the left IFG is associated with the limb apraxia plus gesture discrimination deficit.
    - Voxel-based lesion-symptom mapping analysis showed the same result.

Damage to the Inferior Frontal Gyrus Is Not Correlated with Action Understanding Deficits

- Pazzaglia et al. (2008)
  - However..



Dark square:
without gesture recognition deficits
Lighter circle points:
with gesture recognition deficits.

  - examination of the relation between the amounts of damaged (lesion) tissue in IFG & gesture discrimination scores of patients with gesture discrimination deficits showed no relation.
  - Therefore, IFG involvement doesn't predict gesture discrimination performance

Generalization of the Mirror System to Speech Recognition Fails on Empirical Grounds

- MN & Speech Perception
  - Rizzolatti & Arbib, 1998; Gallese et al., 1996
  - Rizzolatti et al. suggested: MN may underlie the perception of speech gestures.
    - [based on the motor theory of speech perception (Liberman & Mattingly, 1985; Liberman et al., 1967), which has been abandoned among the majority of speech scientists when MN were discovered]

- <u>The motor theory of speech</u>
  - (says) damage to the motor speech areas should produce speech recognition deficits
  - (facts) damage to the motor speech areas do not typically lead to speech recognition deficits
    - motor speech function is dissociated with speech understanding

Syndrome that demonstrate dissociability of motor speech function & speech understanding

① Paul Broca's original case / Broca's aphasia

- Leborne could produce "tan" & "understood what was said to him" (p. 63) (Broca 1861/1960)
- Moineau, Dronkers, & Bates (2005):
  - "Reported that Broca's aphasics were indistinguishable from control subjects on an auditory word comprehension test involving 236 items"
- Dronkers, Redfern & Knight (2000); Damasio, 1991, 1992
  - "Lesions associated with Broca's aphasia tend to be relatively large, involving most of the lateral frontal lobe, motor cortex, and anterior insula but often also extending posteriorly to include the parietal lobe"

- The entire left hemisphere MNS can be affected in Broca's aphasia

Syndrome that demonstrate dissociability of motor speech function & speech understanding

① Paul Broca's original case / Broca's aphasia

Discussion (important notes)

- What's typically ignored:
  - speech comprehension abilities of Broca's aphasia
    [by proponents of motor theories of speech recognition, incl (Galantucci et al., 2006)]
- What's more noted:
  - Broca's aphasics can be impaired on syllable discrimination tasks
    - the ability to judge whether pairs of nonsense syllables are the same (/ba/–/ba/) or different (/ba/–/da/) (Blumstein, 1995).

Syndrome that demonstrate dissociability of motor speech function & speech understanding

② Mixed Transcortical Aphasia ("isolation of speech zone")
(Bogousslavsky, Regli, & Assal, 1988; Geschwind, Quadfasel, & Segarra, 1968)

- Characterized by:
  - severe deficit in speech comprehension, despite the well preserve ability to repeat speech
  - sensory-motor functions of speech are intact
  - system involved in mapping speech onto conceptual-sematic representations is disrupted
- Damaged area:
  - left frontal and posterior parietal regions, with sparing of peri-sylvian speech-related area (such as Broca's area, superior temporal gyrus and the tissue in between)
- indicates that:
  - preservation of motor speech function is neither necessary nor sufficient for speech understanding

Generalization of the Mirror System to Speech Recognition Fails on Empirical Grounds

- Short Conclusion & Discussion:
  - the motor theory/MN theory of speech perception is incorrect in any strong form
    - (not to say that sensory motor circuits cannot contribute to speech recognition)
  - top-down processes indicated in any frontal circuit (not just motor) may be able to influence speech recognition to some extent via sensory-motor circuits.

What Role does the "Mirror System" Play in Action Understanding?

- The MNS isn't the basis for action understanding

  (in the domain of manual gesture & speech)

- What does the MNS reflect?

  (as suggested by Mahon & Caramazza, 2008)

  ① pure Pavlovian association; sensory-motor pairings

  - arg: MNS activity can be dynamically remapped with training (Catmur et al., 2007)

What Role does the "Mirror System" Play in Action Understanding?

- What does the MNS reflect?
  - ② "motor knowledge can influence or augment action "understanding" to some degree, but without committing to the empirically untenable position that action understanding is dependent on the motor system"
    - E.g., concept of "saxophone playing"
    - The how-to knowledge/sensory-motor knowledge can augment the abstract concept by providing a specific sensory-motor association
    - It might even lead to a different "understanding" of the action
      - e.g., knowing whether the player is an expert or not
      - generate prediction about subsequent (the next) actions that could influence sensory systems in a top-down fashion and facilitate subsequent perceptual recognition.

What Role does the "Mirror System" Play in Action Understanding?

- Discussion
  - Although it seems possible that motor experience can augment conceptual understanding in some situations, in others, mirror-like activity appears to reflect sensory–motor associations that are devoid of meaningful conceptual content.
    - "Mirror system" activity that has been observed during the imitation of meaningless gestures (Iacoboni et al., 1999)
    - The demonstration that "mirror activity" associated with viewing actions can be remapped such that it becomes associated with a completely different action (Catmur et al., 2007)
- Thus, perhaps both of the possibilities raised by Mahon and Caramazza apply to the "mirror system."

Conclusion

Thank you