COSC421: Neural Models of Language

Lecture 4: The ‘who’ pathway, and sequential structure in the reach-to-grasp system

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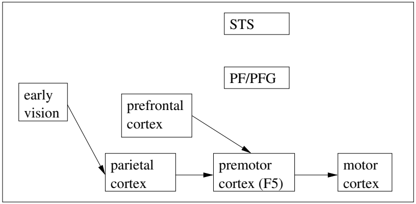
Outline of today's lecture

A problem for the mirror system

The circuitry for action execution looks like this:



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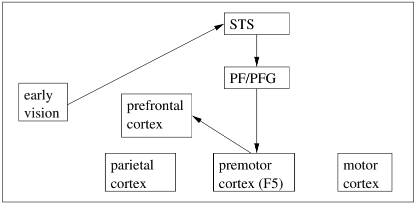
The circuitry for action recognition looks like this:



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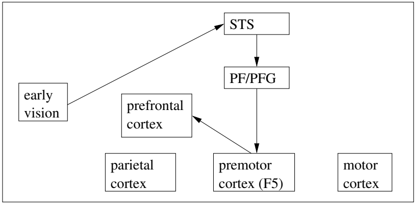


Question: how do we know whether we're representing our own action or that of someone else?

Brain areas active in action execution/observation

Are there any brain areas which are more active during action execution than action observation, or vice versa?

- An obvious idea: Action execution involves the motor cortex; action observation involves STS.

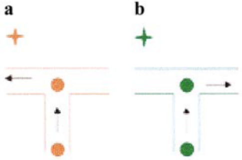
But:

- We often watch our own actions. (So STS is often also active during action execution.)
- Our body is often moving while we watch someone else's action. (We don't attribute the observed action to ourselves in this situation!)

Brain areas associated with the 'experience of agency'

Farrer and Frith (2002) attempted to manipulate 'sense of agency' while controlling for all other sensory/motor factors.

- Subjects used a joystick to drive a circle along a T-shaped path.
- The visual stimulus they saw was either generated by their own movement, or a (different) movement made by the experimenter.

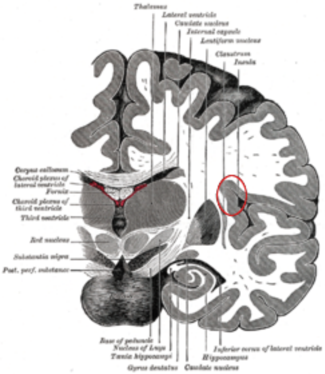


- They saw a movement, and made a movement, in both cases.
- But they only experienced a **'sense of agency'** in the former case.

Brain areas associated with the ‘experience of agency’

Results:

- The experience of agency was associated with activity in the **anterior insula**.

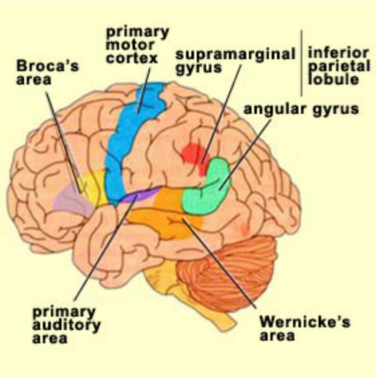


(The insula is a region of cortex that lies inside the lateral sulcus.)

Brain areas associated with the 'experience of agency'

Results:

- The feeling of 'watching someone else's action' was associated with activity in an area of the inferior parietal cortex called the **angular gyrus.**



Some other findings about the anterior insula

Blakemore *et al.* (2005) investigated a patient who had **vision-touch synesthesia**: she experienced tactile sensations when she *saw* people being touched.

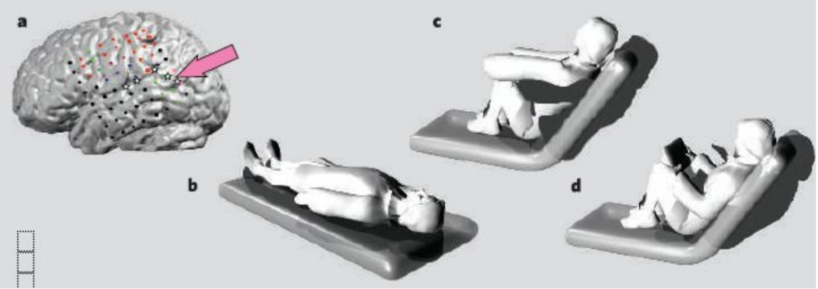
- This patient showed abnormally high activity in the anterior insula. (As well as in somatosensory cortex and premotor cortex.)

If anterior insula activation is associated with self-attribution:

- Abnormally high insula activity might cause an observed touch action to be registered as an 'experienced' action.
- Activation in premotor/somatosensory cortex might be the result of this.

Some other findings about the angular gyrus

Arzy *et al.* (2008) found that stimulating the (left) angular gyrus in an epileptic patient caused her to hallucinate the presence of a person 'right behind her', in the same posture as herself.



If activity in the angular gyrus indicates 'action observation mode', maybe stimulating it causes her to interpret proprioceptive information about her own body as information about someone else.

Some other findings about inferior parietal cortex

Schizophrenia is a condition where attributions of agency to self and other are often confused.

- Some schizophrenics show ‘passivity’—a condition where they think their own actions are under control of an external agent.
- Such patients have increased activation of inferior parietal cortex.

If IP cortex activation is associated with attribution of an action to others, perhaps abnormally high IP activation is the cause of passivity phenomena.

The ‘match’ model of action attribution

How do we attribute agency to ourselves or to others?

One idea: the sense of agency results from a *match* between signals generated in the motor system and signals arriving from perceptual (visual/somatic) sources.

- Nielsen (1963): subjects identified an observed hand as their own if its actions were correlated with their motor commands.
- Recall the lecture on motor control: an **efferent copy** of motor commands is given to a **forward model**, which calculates its expected sensory consequences.

Maybe we attribute an evoked premotor signal to ourselves if the sensory stimuli we experience are those which are predicted from this motor signal.

The ‘match’ model of action attribution

One problem: according to our model of the mirror system, we expect correlations between visual stimuli and motor signals whether we perform an action ourselves, or watch another agent performing it.

One way to save the match model of agency: the perceptual stimuli have to be *somatosensory*, not visual.

- Normal agents only experience somatosensory stimuli when they perform an action.
- So maybe the anterior insula is involved in detecting a match between motor signals in premotor cortex and reafferent *somatosensory* signals.
- Note: the anterior insula does receive a lot of somatosensory information.

The ‘match’ model of action attribution

So why is the inferior parietal cortex active when we attribute an action to someone else?

Recall:

- Inferior parietal cortex is on the ‘action recognition’ pathway (STS$\rightarrow$PF/PFG$\rightarrow$F5)
- Posterior parietal cortex is on the ‘action execution’ pathway
- Maybe these pathways compete with one another, with high IP activation favouring action recognition.

Problems with the ‘match’ theory of attribution

1. The issue of whether somatosensory signals match motor signals feels more like a *consequence* of a decision about who the agent is, not its cause.

2. Models of the mirror system all assume that there are two separate modes: recognition mode and execution mode.

- The circuitry of the system is completely different in the two modes.
- There should be explicit mechanisms for *selecting* one mode or another, so that (e.g.) the agent can learn when to act and when to observe.

Problems with the ‘match’ theory of attribution

3. The match theory provides a means for distinguishing between onesself and external agents, but it doesn’t specify how we distinguish *between different external agents*.

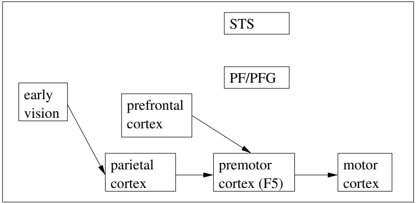
- Presumably we have to identify the agent using the object classification pathway in IT. But how does this process relate to the process of action monitoring?

4. We can *imagine* actions, or *remember* actions, without there being any somatosensory stimuli at all.

- We have no problem at all distinguishing between our own actions and those of others in such situations.

The ‘mode-setting’ model of action attribution

The circuitry for the mirror system can be set up in two ways:



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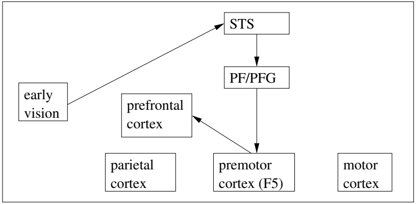


The ‘mode-setting’ model of attribution

I suggest that there are special operations which put our mirror system into ‘recognition mode’ or ‘execution mode’.

The operation which puts us into recognition mode is an **action of attention to an external object**.

- The object captures our attention, because it is salient. This puts us into action recognition mode.
- Thereafter, this object will be understood as the agent of any action evoked in our mirror system.
- Attending to the object also provides us with an opportunity to categorise it.

The operation which puts us into execution mode is a **decision to act**.

The mode-setting model of attribution

This mode-setting model of attribution solves the problems raised by the match model.

- The agent can now learn when to act and when to observe.
- The agent can distinguish between different external agents.
- In order to distinguish between self and other in imagined or remembered actions, the agent can *simulate* the operations of moving into action execution or action recognition mode.

What's a 'decision to act'?

Is it really plausible that agents 'decide to act', prior to deciding what action to do? Here's some evidence.

- If you record EEG signals from a subject and ask them to make a spontaneous movement, you see a wave of activity in precentral and parietal areas which precedes the action, called the **cortical readiness potential** (Shibasaki 1992). It's the same for all actions.
- There is a second EEG signal called the **lateralised readiness potential** which occurs later in action preparation, and which reflects which hand will be used.
- Incredibly, the general readiness potential occurs *before the agent is aware of their decision to act* (Libet *et al.*, 1983).
- The lateralised readiness potential occurs *after* the agent becomes aware of their decision (Trevena and Miller, 2002).

EEG signals in observed and imagined actions

The EEG signals which precede the observation of an action are very different from those which precede the execution of the same action (Babiloni *et al.*, 2003).

However, the EEG signals which precede the *mental simulation* of an action are quite similar to those which precede actual execution of the action (Jankelowitz and Colebatch, 2002).

- In fact, there are surprisingly few differences between neural activity for actual and simulated actions.

The crucial question: are there differences between *imagining executing* an action and *imagining observing* the same action?

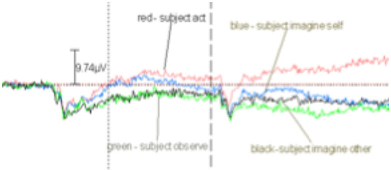
EEG signals in observed and imagined actions

We did a preliminary EEG study to look at this question.

Subject and experimenter sat on opposite sides of a table, with a cup in the middle. A preliminary signal indicated one of four conditions:

Subject grabs cup	Experimenter grabs cup
Subject imagines grabbing cup	Subject imagines exp'ter grabbing cup

The action (real or simulated) was triggered by a second signal.



Between the two signals, there's a main effect of agent (self vs other), but not of modality (actual vs imagined).

Mode-setting and match models combined

Problem for the mode-setting model:

- It doesn't seem to explain the difference between the two conditions in Farrer and Frith's experiment.
  (In each condition, the subject presumably 'decides to act', but there's only a 'sense of agency' in one condition.)
- The 'sense of agency' is much better explained in terms of the match model.

One way of reconciling the two models: distinguish between the *experience* of agency and the *representation* of agency.

- We only get the *experience* of agency when we actually act.
  (When we simulate an action we don't get it.)
- To *represent* agency, we need to make reference to a mode-setting operation.

Summary

- Babies have to *learn* a concept of 'self'.
- They also have to develop concepts of other agents.
- These concepts seem to be *acquired* using correlations between perceptual and motor signals.
- During actual experience, correlations between motor signals and reafferent *somatosensory* signals appear to be associated with a sense of agency.
- But I suggest that the main mechanism for distinguishing between one's own actions and those of others is a 'mode-setting' operation, which configures the circuitry in the mirror system for action execution or action observation.

Outline of today's lecture

1. The problem of action attribution in the mirror system
2. Sequential structure in experience of reach-to-grasp actions
3. Attention to the agent and patient during experience of an action
4. Summary

The aim for the rest of the lecture

Here's what I want to persuade you:

- The process of executing a reach-to-grasp action has a characteristic **sequential structure**.
- The process of perceiving a reach-to-grasp action also has a characteristic sequential structure.
- Except for the first item, the sequences for execution and perception are basically the same.
- In each case, the agent and target of the action are each attended to *at two different times*.

Definitions: an observer and an agent

We'll define someone called the **observer**, who either executes the reach-to-grasp action or perceives it.

> *Note: if he executes the action, he still observes it (from the perspective of the agent).*

We'll define the **agent** as the one who executes the action. Thus:

Action execution	Action perception
observer $=$ agent	observer $\neq$ agent

The decision to act or to observe

To begin with, envisage a context where the observer hasn't *decided* whether to establish action observation mode or action execution mode.

- This is a decision that has to be made: you can't be in both modes!

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My suggestion:

- Experiencing a reach-to-grasp action must always *begin* with a mode-setting operation.
- Establishing action execution mode is like 'attending to yourself' as an agent.
- Establishing action perception mode happens through attention to a salient *external* agent.

The decision to act

When an observer decides to act, he enters a cognitive mode where perceptual stimuli aren't just seen as interesting things to look at: they're treated as *potential targets for motor actions*.

- In this mode, each region in the saliency map is mapped to a 'reach' movement vector, and one is selected as a target (see Lecture 2).

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Before the observer has decided between execution and perception modes, salient locations are not reach targets: they are potentially interesting objects in the world.

Proposal: attending to a salient location at this point should *trigger* the establishment of perception mode.

- The observer is interested in the object in its own right—that includes its properties, but also its actions.

An asymmetry between deciding to act and to observe

'Deciding to act' is like *attending to onesself* as an 'interesting' object.

I suggest:

- 'Deciding to observe' happens when we attend to an external object.
- 'Deciding to act' is a special case, when we attend to ourselves.

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Note:

- A ‘decision to observe’ shifts attention away from onesself.
- A ‘decision to act’ tells us that the agent of the forthcoming action will be onesself.

Summary

The observer begins in a null context, where perceptual stimuli inform a decision to act or to observe.

- A 'decision to act' configures the observer's mirror system for action execution.
  The observer only selects an object as a target *after* having decided to act.
- A 'decision to observe' configures the observer's mirror system for action recognition.
  It is triggered by attention to an object. (Which will end up being the object the observation is 'about'.)

I'll now consider action execution and action recognition separately.

1. Action execution

When the observer has decided to *act*, he has two further decisions:

- What object(s) is he going to act *on*?
- What motor programme is he going to execute?

Note: deciding on an object *as a target* means choosing a movement vector in the 'reach' motor pathway. Choosing a *motor programme* involves more than this: we need to choose a hand trajectory and a finger preshape sequence.

I suggest: he has to choose a target before choosing a motor programme.

Choosing a target > choosing a motor programme

Some arguments:

- Agents typically attend to a target they reach for very early in the reach trajectory (see e.g. Johansson *et al.*, 2001)
- Selecting a reach target triggers a shift of visual attention to this target (see e.g. Schneider & Deubel, 2002). The link probably involves F7v, the supplementary eye fields.
- Many computations in the 'grasp' pathway presuppose that the target is attended to. (E.g. computing the shape of the object requires attention to the object.)
- In macaque, many 'canonical neurons' in F5 only activate if the monkey fixates an object requiring the associated grasp (see e.g. Gallese *et al.*, 1996).

2. Action perception

When the observer has decided to *observe*, he must determine two things:

- What object(s) the observed agent is acting on (if any)
- What the observed agent's motor programme is (if anything)

I suggest: if the observed action is a reach-to-grasp, the observer identifies the target of the action before classifying the action.

Attention to the target > classifying the action

Some arguments:

- Observers of a reach-to-grasp action saccade to the intended target *early* in action monitoring (Flanagan and Johansson, 2003).
- Many mirror neurons don't fire if their associated action is 'pantomimed', without a target object (Gallese *et al.*, 1996).
- Computational models of action recognition tend to assume that observers represent the trajectory of the hand *in relation to the target*. (See e.g. Oztop and Arbib, 2002).
- It's hard to see how the mirror system can be trained unless the observer of an action establishes joint attention with the agent.

Some more supporting data

Attention to agent $>$ attention to target:

- Webb *et al.* (2010): observers reliably saccade to the agent of an observed reach-to-grasp action, and then to the target. (Again, the target saccade is anticipatory.)

Attention to agent $>$ classifying the action:

- Nelissen *et al.* (2005): most F5 mirror neurons only respond to an action if the agent of the action is in view. (They don't respond to 'disembodied arms'.)

Summary

Action execution:

- Attention to agent $>$ attention to target (as a target)
- Attention to target $>$ activation of motor programme

Action observation:

- Attention to agent $>$ attention to target
- Attention to target $>$ activation of motor programme

Summary

If an observer *O* executes the action of grabbing a cup:

- *O* attends to himself.
- *O* attends to the cup (as a target).
- *O* activates the ‘grab’ motor programme.

If *O* perceives an external agent *A* grabbing a cup:

- *O* attends to *A*.
- *O* identifies *A*’s intention, and attends to the cup.
- *O* activates the ‘grab’ motor programme.

Some objections: action observation

Does observing a reach-to-grasp action *have* to involve that sequence?

- Surely I can recognise an action even if I don't see the agent?
- Surely I can look at the target first, and then look at the agent?
- Surely I can recognise an action from a still picture?

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- Surely I can recognise an action from a still picture?
  But there's a difference between *perceiving* an action and *inferring* it.

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  The 'intention to grab a cup' is probably an intention to do a sequence of things: first find a cup, then grab it.
  Also, the *specific grasp action* can only be selected when you know what you're grasping for.

Some objections: action observation/execution modes

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E.g. playing tennis / fighting?

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  Some dual tasks are performed by switching rapidly between tasks.**

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  John fought Mary
  John and Mary fought...

Outline of today's lecture

Actions and their reafferent feedback

A SM action signal should be distinguished from the perceptual signals which result from its execution.

For attentional actions:

- An action signal is a direction of attention;
- Reafferent feedback is a representation of the attended object.

For motor actions:

- An action signal is the activation of a motor programme in (pre)motor cortex;
- Reafferent feedback might include a representation of the agent *as an agent*.

The role of reach-to-grasp actions in creating crossmodal object representations

We need to represent an agent *as an object* and *as an agent*.

We need to represent a target *as an object* and *as a set of motor affordances*.

- A reach-to-grasp action involves attending to the agent in both ways. It provides an opportunity to learn the associations between them.
- Ditto the target.

The ‘stable grasp’ state

If the observer successfully performs a reach-to-grasp action, he achieves a **stable grasp** state. This is particularly useful for learning a cross-modal representation of the target.

- The observer can learn to map a *visual* representation of the **location** of the grasped object to the current *motor* representation of the position of his hand.
- The observer can learn to map a *visual* representation of the **shape** of the grasped object to the current *motor* representation of the shape of his hand.

Static and dynamic agent representations

An agent is an ‘object’: recognisable by a characteristic pattern.

An agent is also a dynamic entity:

- An **articulated** entity, which moves in certain characteristic ways.
- An entity associated with particular **dispositions to act**. (Not all agents act the same way in the same circumstances!)

An observer needs to relate these concepts together, so when he attends to an agent he can predict how s/he will act.

Outline of today's lecture

The sequence for perception of a reach-to-grasp

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State 3	As a corollary of this process, *O* re-attends to the agent *as an agent*.
State 4	*O* re-attends to the cup, in the course of perceiving the agent establishing a stable grasp.

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State 2	*A* receives feedback from this operation: the percept ‘cup’.
Operation 3	*A* selects an action category (‘grab’) and begins to execute the grab action.

The sequence for execution of a reach-to-grasp

Operation 1	*A* attends to himself, configuring his mirror system circuit for action execution.
State 1	*A* receives reafferent feedback that this operation succeeded.
Operation 2	*A* selects an object to reach for (the cup), and hence executes an action of attention to the cup.
State 2	*A* receives feedback from this operation: the percept ‘cup’.
Operation 3	*A* selects an action category (‘grab’) and begins to execute the grab action.
State 3	*A* receives feedback from the process of action execution, which includes a percept of himself ‘as an agent’.

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State 3	*A* receives feedback from the process of action execution, which includes a percept of himself 'as an agent'.
State 4	*A* re-establishes the cup in the haptic modality.

SM signals during experience of a reach-to-grasp

	Transient signals	
	Action signals	Reafferent signals
	attend_agent	*attending_to_agent*
	attend_cup	*attending_to_cup*
	grasp	*attending_to_agent*
		attending_to_cup

Deictic routines

Ballard *et al.* (1997) noticed that many cognitive processes are *inherently sequential*.

- The representations in 'perceptual' neural areas are transitory: they reflect the agent's current focus of attention.
- The information in one transitory representation is used to work out the next attentional action.
- A **deictic routine** is a sequence of transitory neural representations linked by attentional actions $R_1, A_1, R_2, A_2, R_3, A_3 \ldots$
  - R_i enables A_i. A_i brings about R_{i+1}.
- To express the 'meaning' of a transitory neural representation, we must often make reference to the deictic routine which brought it about.

A big hypothesis

Hypothesis:

The process of experiencing an action is organised as a deictic routine.