A Simple Model of Cortical Activations During Both Observation and Execution of Reach-to-Grasp Movements

Matthew Hartley and John G. Taylor

King's College London, The Strand, London, WC2R 2LS
`mhartley@mth.kcl.ac.uk, John.G.Taylor@kcl.ac.uk`

Abstract. We discuss evidence for the existence of mirror systems in the brain, including recent experimental results that demonstrate the use of shared pathways for the observation and execution of reaching and grasping actions. We then describe a brain based model of observational learning that explains the similarities and differences in levels of activation of brain regions during observation and execution of actions. We simulate a very simple paradigm whereby an actor performs an action which is observed and then repeated by the simulated animal. We discuss the implications and possible extensions of our model.

1 Background

1.1 Mirror Systems in the Brain

There is considerable evidence for the existence of "mirror systems" in the primate brain - areas activated both in the production of actions and observation of those actions in others [5,12]. These were first discovered in the F5 region of the monkey cortex (known to be involved in formation of grasping movements) and inferior parietal and thought to be confined to those areas.

More recent studies [11] (and unpublished data) have shown that mirror activity in the brain is widespread, and substantial parts of the action execution pathway are activated during observation tasks. In particular, the primary motor and somatosensory cortices (M1 and S1) are activated during observation of movements. This suggests that our understanding of the motor actions of others requires us to "mentally simulate" those actions using parts of cortical (and possibly sub-cortical) circuitry that would be used for the production of these actions [13].

While single cell recording studies examine monkeys, there is evidence from imaging studies that similar mirror systems exist in the human brain - for example, substantial evidence that viewing hand movements activates sensory cortex [1] and that viewing of speech activates speech production regions [15].

1.2 Existing Models of Imitation

There are a number of existing models of imitation/observational learning. Broadly, we can divide these models into two categories - those involving

J. Marques de Sá et al. (Eds.): ICANN 2007, Part II, LNCS 4669, pp. 899–911, 2007.

machine learning approaches and those that involve coupled forward and inverse models for motor control. The models often address mirror neurons specifically, rather than a particular focus on observational learning, but provide valuable insight nonetheless.

Of the machine learning variety, examples include [14] which uses a dynamical systems approach to organise observation and execution of dynamical actions and examines how these can share components, and [2], which uses evolutionary algorithms to develop behaviour of agents which react to teaching agents by generating outputs. For more details of computational mirror neuron models, see [10] for a recent summary.

The coupled inverse/forward model approach is popular since it extends existing attempts to understand motor learning - see [16], [4], [8], [3] for details of how brain based motor control might operate. For examples of this type of model see [6], the Mosaic model which is a well developed motor control model extended to mirror neurons/imitation and [9] a model of infant grasp learning that makes use of motor control circuitry. The coordinate systems between which these models transform are often not entirely clear. Some models suggest a transformation from Euclidean space coordinates to joint angle coordinates taking place in premotor/parietal areas, however experimental evidence for this is lacking, and most data seem to suggest that coding in premotor cortices is related to direction of action in Euclidean space [7].

Another interpretation of the concept of internal models is that, rather than always necessitating a conversion from physical to muscle/joint space coordinates, they are involved with the transformation of goal and current state to the action necessary to achieve that goal. In this case, some of the role of premotor/parietal regions in the transformation of current hand/arm state and desired affordances on an object into direction vectors for movement could be considered to be part of an inverse model system.

1.3 Problems to Address

The biggest questions to be answered by a model of neural activation during observation are:

Why is there so much activation of brain regions associated with the execution of movement during observation of those same movements?

In particular, how is S1, the primary somatosensory cortex, activated during observation (since this area involves sensorimotor feedback, which is obviously not present during observation)?

It seems reasonable to assume that part of the reason for extensive co-activation of motor pathways during action and observation is that attempting to understand the movement observed requires use of the same circuitry for executing movements. This may also explain why activation of motor regions is not always seen during observation of reaching movements, since unless there is sufficient reason to attempt to understand the movements, the brain circuitry is not recruited.

The activation of S1 is in some sense more puzzling, since it is considered to be activated primarily by proprioceptive feedback from muscles, which does not occur without execution of movements. One possible suggestion is that the region is involved with preservation of “sense of self” during observation of movement and general attribution of agency, but this does not explain how it is activated. For there to be S1 activation during observation of movement, something must be providing a substitute for proprioception, since muscles are not active. The neural projection from M1 to S1 is a candidate for filling this role, and we suggest this as a reason for the activation, as we will see below.

2 Model Details

Our model comprises several modules, here we describe their individual function. A diagram of the model can be seen in Figure 1. Some of these modules correspond to clearly identifiable brain regions (the visual system, M1 and S1 for example), others, such as sensorimotor integration and extraction of affordances correspond to several related areas.

Visual system. We assume that considerable low level visual processing takes place before input to our system, such that inputs occur as processed spatial coordinates. The visual system then allows observation of actions, determination of goal end points and observation of instructions to perform actions.

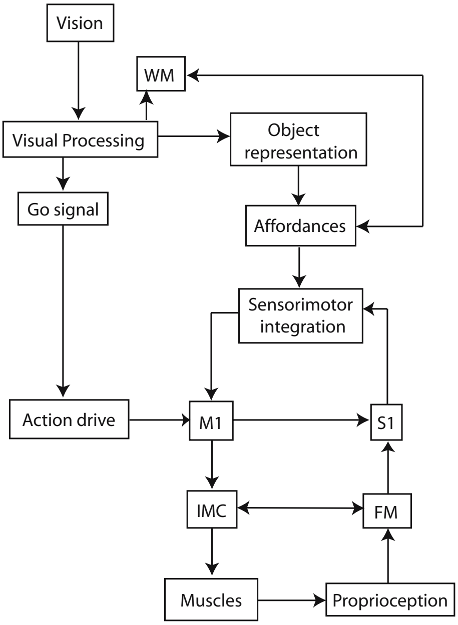

Fig. 1. Model structure details showing the connectivity of the regions used in the model

Object representations. Input from the visual system activates an object representation in this module, each possible object occurring as a dedicated single node (graded neuron).

Working memory. The WM serves to store the coordinates observed contact points in physical space during observation of actions.

Action drive. The action drive provides the reason for which the simulated animal performs an action. The drive arises from some presumed association of goal end points with food rewards (based on previous training). The action drive is modelled as a single graded neuron that is activated by the go signal.

Affordances. This module is involved in extracting affordances from objects, based on the way the object is to be used, and the observed actions on the objects. In this simple simulation, we assume that affordances take the form of a contact point on the button to be pressed.

Sensorimotor integration. Here the target of movement (the contact point generated by the affordances module) is integrated with sensory feedback about the current position of the hand to form a motor plan to reach the target. This output takes the form of a direction vector for movement to M1.

M1. The primary motor cortex receives a movement plan from the IMC and activates the IMC which generates suitable muscle movements from the plan. We model it using a small population of graded neurons that can encode a direction vector.

S1. Primary sensory cortex. It receives input from proprioceptive feedback (via the forward model) to update the position of the arm based on known movements. It also receives an efferent copy of the motor plan from M1. Like M1, it is modelled using a population of graded neurons.

IMC. In the Inverse Model Controller a target direction vector in physical space is converted into the muscle space movements necessary to carry out the planned movement. This involves a conversion from the direction vector input from M1 (coded in Euclidean space) to a code involving the joint angles necessary to perform the movement.

FM. The forward model (FM) takes proprioceptive feedback from the muscles and calculates how this updates the position of the arm. This information is passed to the sensorimotor integration module via S1 so that it can update the motor plan, involving a transformation from joint angle coordinates to the consequent movement of the arm in physical space.

We can use the activation of the parts of the system modelled as graded neurons to compare to experimental results (specifically M1, S1, the object representations, action drive and the affordances extraction network). It is more difficult to make comparisons with non-neural simulated components (the sensorimotor integration module, working memory and inverse and forward models), but we can record when these components are used and generate activation levels based on this usage.

2.1 Identification of Brain Regions Modelled

We can consider which brain regions might correspond to some of the components of our model. This allows us to compare to imaging data which include activations, and also to make predictions. We can see these allocations in Table 1.

Table 1. Identification of model components with brain regions

Model area	Brain region
Working memory	Prefrontal cortex (PFC), parietal lobe
Object representations	Superior Temporal Sulcus (STS), temporal lobe (TL)
Affordances	Parietal lobe
Sensorimotor integration	F5 and other premotor areas
IMC and FM	Brainstem (possibly also cerebellar/striatal network)

3 Simulation Paradigm

We consider initially a very simple simulation paradigm. The environment consists of an actor which contributes only by performing actions which can be observed by the simulated learner. Both actor and learner have a simple rod-like arm with a single joint of variable angle. The environment also contains a button object which can be reached by both actor and learner by arm movement. We assume that this object has some previously associated value (such as association with a food reward) which causes it to be of interest to the learner. When this joint reaches a certain angle θ, the arm is in contact with the button object and is considered to have reached it.

The simulation then consists of two stages:

Stage 1: The actor makes an arm movement terminating at the location of the button. This action is observed by the learner, and we record the activation of the various model regions. The learner also registers the location of the button and the point of contact used.

Stage 2: The learner repeats the previously observed movement, terminating at the button. Again we record activation of the model regions which we can then compare to the observation phase.

The simulation sees the teacher's actions from the point of view of the learner. We assume that because our very simple model consists of a single arm only, the issue of translating the actor's movement into an egocentric perspective is absorbed into some stage of visual processing.

These stages can be seen in Figure 2.

3.1 The Simulation During Observation

During observation of action, the visual system passes on the observed object to the object representation module, and the contact points to the working

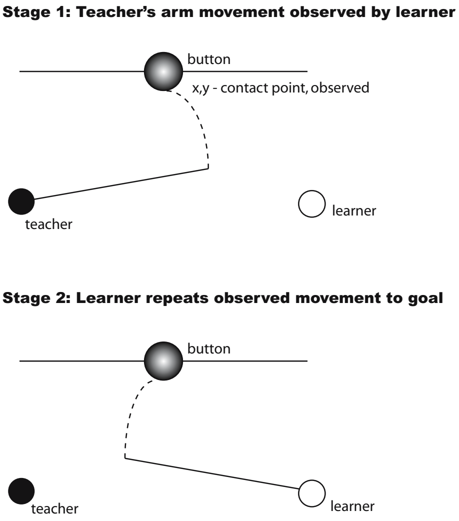

Fig. 2. Explanation of paradigm stages showing the simple actor and learner components and the action involved

memory. The contact points from the working memory are integrated with those generated by previous association of the object, and the result passes to the sensorimotor integration module. This output from this is fed both to M1 (where it is insufficient to actually cause muscle activation) which also activates S1.

3.2 The Simulation During Execution

During execution, the observed go signal is processed by the visual system and then used to activate both the action drive and the goal module. The visual system also activates the object representation module. The sensorimotor integration module combines information about the spatial location of the contact points with sensory feedback about the current position of the arm and produces a direction vector for movement (by performing a target - hand position calculation). This is passed to M1 and onwards to the IMC which converts it to a suitable set of impulses to muscles. Sensory feedback from muscles returns to the forward model, which calculates the change in arm position implied by the proprioception, and passes this information to the sensorimotor feedback module so the motor plan can be updated.

4 Results

To gain some idea of how well the model replicates experimental data, we can examine activation levels of both M1 and S1 during observation and execution phases. Since these are modelled as graded neurons, we can examine their activation levels to give an indication of that region's output. Each of these has a short "rise time", where the initial inactivity in the model M1 and S1 neurons is raised by the periodic input from the sensorimotor feedback module, whenever it recalculates the motor plan.

We are interested in comparing our results to those showing activations of M1 and S1 under observation/execution, which can be found in [11] and are reproduced here in Figure 3.

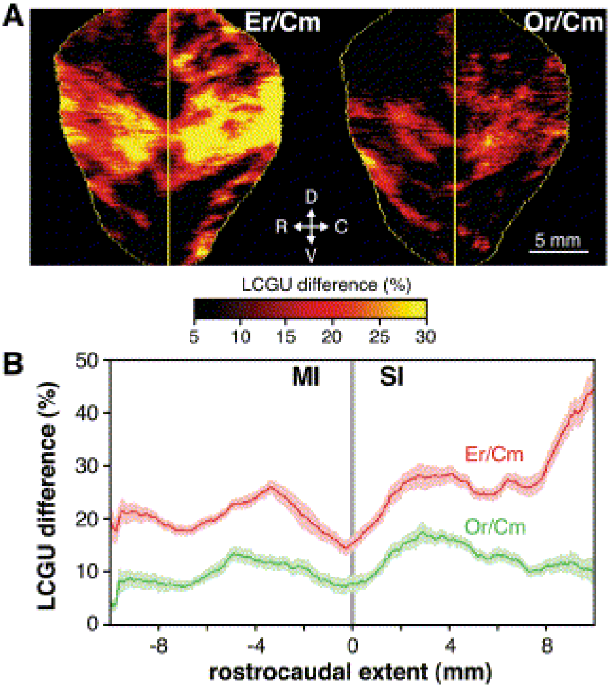

Fig. 3. Cortical activity of S1 and M1 during both observation and execution (showing percentage differences in activation) of reach-to-grasp movements, taken from [11]. A: Maps of activations in M1 (left) and S1 (right) showing execution of grasping (Er) and observation of grasping (Or) compared to biological motion control (Cm). B: Percent differences in activation over the anterior-posterior extent of M1 and S1 where -10 is the anterior crown, +10 the posterior crown and 0 the fundus. Data use local cerebral glucose utilisation (LGCU) values, and were recorded with the quantitative 14C-deoxyglucose method.

4.1 M1

In Figure 4 we see how activation of M1 during execution of the action is higher than activation during observation. Each 250ms, the motor plan is recalculated and the direction vectors for movement are fed to M1 causing activation, this being smoothed by the neuron's response time. The higher activation during execution occurs as a result of the action signal fed to M1.

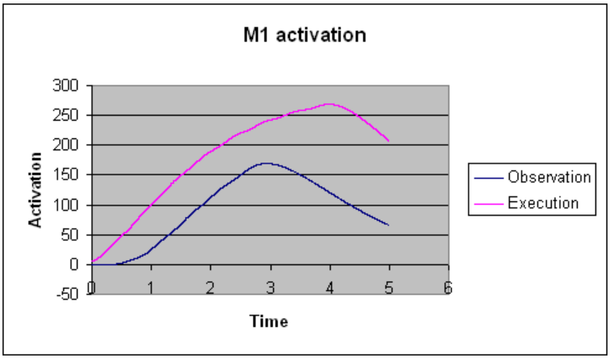

Fig. 4. Activation of our simulated M1 during both action observation and action execution showing activity against time

4.2 S1

Figure 5 shows a similar pattern of activation for S1. S1 receives proprioceptive feedback from muscles (via the forward model), which is why it is activated more strongly during execution of actions.

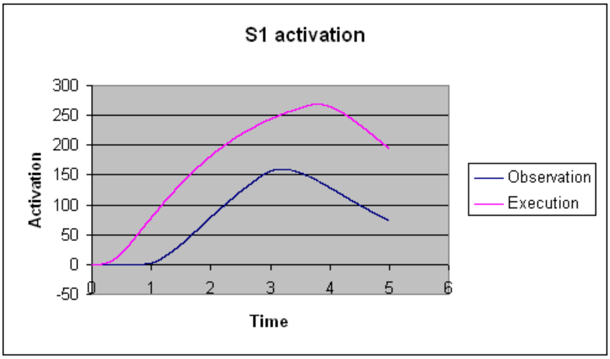

Fig. 5. Activation of S1 during observation and execution phases showing activity against time

4.3 Sensorimotor Integration

We can consider what activation we expect from our sensorimotor region, by considering its activation to increase when it performs a calculation, then to decay exponentially over time between these events. We can see the results of this process in Figure 6 - the peak activation level is similar during execution to integration, although it begins earlier (due to the timing of movement versus observation of that movement), and persists for longer.

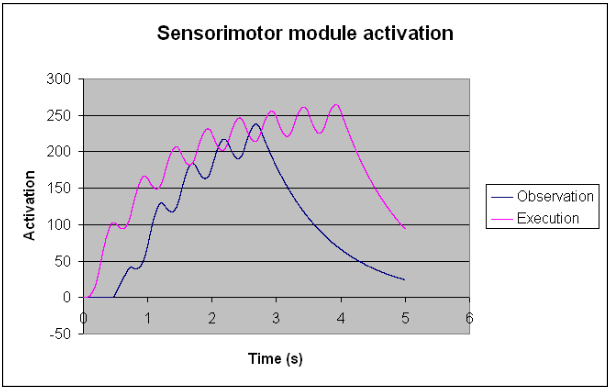

Fig. 6. Activation of sensorimotor region during observation and execution phases showing activity against time

4.4 Summary

The results demonstrate activation of both M1 and S1 during the execution phase of the simulation (as would be expected). They also show activations of both M1 and S1 (at lower levels to the execution case) during the observation phase, a more surprising result. These activations arise from the nature of the model's connectivity (which in turn provides predictions for experiment), as we shall now discuss.

5 Discussion

An important component of the model is the capacity to simulate the sensory consequences of an action that is being observed. This is the reason why activation of S1 occurs in our model during observation (a non-obvious result!), and why there is greater activation during execution, since the input from simulation of the action is added to proprioceptive feedback from muscles.

5.1 Comparison with Experiment - What Our Results Show

The primary areas we use for comparison here are the M1 and S1 regions. As discussed previously, experimental results on monkeys show partial activation of both M1 and S1 during observation of reaching and grasping movements. In these results, M1 and S1 both show significant (above threshold) activity during observation, as we can see in Figure 3. When we compare these to Figures 4 and 5 we see that our model also demonstrates similar lower (but above threshold) activations for M1 and S1 during observation.

It is important to consider what the nontrivial aspects of the results are. Activation of both M1 and S1 during observation of movement is an inherently surprising result and one replicated in our model. Although the reasons these occur (the projection from M1 to S1 to activate S1, and the activation of the sensorimotor system during observation) are relatively simple, they provide predictions for experimental verification (as we describe below).

5.2 Model Predictions

Since one of the key components of our model is the use of the projection from M1 to S1 to activate S1 during the observation stage, we can consider what might happen if that connection were interfered with. In particular, we predict that no activation of S1 would occur during observation.

Another prediction given by our model is that the action drive signal is crucial for the difference between activation of muscles during actual movement and activation that does not cause movement during observation. This is our current answer to the question of why no movement occurs during observation of actions (since motor cortex is activated) - without the action drive there is insufficient. Another possible explanation is that actual movement is inhibited in some way (although since something must be causing this inhibition, these explanations are similar in basic concept, although differ in mechanism).

5.3 Unanswered Questions and Extensions

Some data show that activation of M1 and S1 does not always occur for pure reaching movements. Why this is the case is unclear. One possible explanation is that, unless the movement is of interest (perhaps important to observe since repetition will aid in obtaining a food reward), no attention is paid to the moment. This provokes an interesting question as to how attention interacts with the system, which is an interesting direction for further study.

As mentioned above, we suggest the action drive as an explanation for cause of actual movement. This explanation raises questions as to what controls this action drive and to whether is operates directly by providing stimulation to muscle controllers, or indirectly by releasing inhibition on muscles.

The existing model is very simple and open to several avenues of extension, in particular more neurophysiologically realistic modelling of the sensorimotor integration module. Currently this performs non-neural calculations based on deriving the target vector from the target contact points and information about current hand position. It may be possible to use a trainable network here, although that would add a large degree of complexity. The F5 region of the brain is thought to be involved (possibly along with other premotor areas) in the target - hand calculation, and it may be possible to examine further biological data here to suggest suitable mechanisms.

Another possibility for extension is to a more complicated paradigm - a simple reach to a button position provides a basic demonstration of the model's operation. However, there is some question as to the difference in motor/sensory cortex activation during the observation of reaching and grasping (vs. purely reaching) movements. A paradigm involving full reaching and grasping (as separate movements) would allow us to cover this situation.

6 Conclusion

Our approach is that of "functional modelling", in that we assume certain functional modules are needed for the overall process, and then relate to brain science results to locate these functional modules in connected sets of brain modules. The set of modules are then simulated and compared to further details of experiment.

In our model, the activation of M1 and S1 during both action and observation arises because the same cortical circuitry is activated in both situations from visual input coupled with a need to understand the nature of the observed movement. S1 is activated during observation because of the projection from M1 (which is active as part of the process of observing movement in a manner intended to extract information. Actual motor action occurs because an action drive signal is necessary to provide sufficient motor cortex activity (and possibly also to release inhibition of actual movement).

Our model extends existing research by providing an explanation for the unexpected activation of motor and sensory cortices during observation of reaching and grasping movements. We also provide a very simple experimentally testable mechanism for the production of the activation of S1 during observation of movements.

References

1. Avikainen, S., Forss, N., Hari, R.: Modulated activation of the human SI and SII cortices during observation of hand actions. Neuroimage 15, 640–646 (2002)
2. Borenstein, E., Ruppin, E.: The evolution of imitation and mirror neurons in adaptive agents. Cognitive Systems Research 6 (2005)
3. Davidson, P.R., Wolpert, D.M.: Widespread access to predictive models in the motor system: a short review. J Neural Eng 2, 313–319 (2005)
4. Desmurget, M., Grafton, S.: Forward modeling allowed feedback control for fast reaching movements. Trends Cogn Sci 4, 423–431 (2000)
5. Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G.: Action recognition in the premotor cortex. Brain 119, 583–609 (1996)
6. Haruno, W., Wolpert, D.M., Kawato, M.: Mosaic model for sensorimotor and learning control. Neural Computation 13, 2201–2220 (2001)
7. Kakei, S., Hoffman, D.S., Strick, P.L.: Direction of action is represented in the ventral premotor cortex. Nat Neurosci 4, 1020–1025 (2001)
8. Mehta, B., Schaal, S.: Forward models in visuomotor control. J. Neurophysiol 88, 942–953 (2002)
9. Oztop, E., Bradley, N.S., Arbib, M.A.: Infant grasp learning: a computational model. Exp Brain Res 158, 480–503 (2004)
10. Oztop, E., Kawato, M., Arbib, M.: Mirror neurons and imitation: A computationally guided review. Neural Netw 19, 254–271 (2006)
11. Raos, V., Evangeliou, M.N., Savaki, H.E.: Observation of action: grasping with the mind's hand. Neuroimage 23, 193–201 (2004)
12. Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L.: Premotor cortex and the recognition of motor actions. Brain Res Cognit 3, 131–142 (1996)

13. Rizzolatti, G., Fogassi, L., Gallese, V.: Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Rev Neurosci 2, 661–670 (2001)
14. Tani, J., Ito, M., Sugita, Y.: Self-organization of distributedly representated multiple behavious schemata in a mirror system: Reviews of robot experiements using RNNPB. Neural Networks 17, 1273–1289 (2004)
15. Watkins, K.E., Strafella, A.P., Paus, T.: Seeing and hearing speech excites the motor system involved in speech production. Neuropsyhcologia 41, 989–994 (2003)
16. Wolpert, D.M., Ghaharamani, Z., Flanagan, J.R.: Perspectives and problems in motor learning. Trends Cog Sci 5, 487–494 (2001)

A Appendix

A.1 Model Details

Parameters involved are given fully in Table 2.

The simulated M1 and S1 consist of simple graded neurons with membrane potential obeying the equation:

$$C\frac{dV}{dt} = g_{leak}(V - V_{leak}) + I, \tag{1}$$

where I is the neuron's input current. Their output is sigmoidal in form:

$$\frac{1}{1 + exp(-V/V_{scale})} \tag{2}$$

where V_{scale} scales the rate of change of the sigmoid function.

The sensorimotor integration module is represented by a calculating machine that provides a constant activation level when performing a calculation. When it integrates the goal contact points with current sensory information, its activation level is set to Act_{smi}. It performs this transformation every t_{smi} ms, and when it does so, its output becomes SMI_{out} for t_{calc} ms.

The action drive provides a constant current output I_{action} when active. When performing a movement, the muscles have a proprioceptive feedback signal that translates to a current equal to $I_{proprio}$ which is fed to S1.

A.2 Table of Parameters

Table 2 shows the parameters used in the model with units where applicable.

Table 2. Values of constants

Variable name	Value	units
V_{leak}	-70	mV
C	25	nF
g_{leak}	0.025	μS
I_{action}	10	nA
$I_{proprio}$	15	nA
t_{smi}	100	ms
t_{calc}	50	ms
SMI_{out}	5	nA
Act_{smi}	1	n/a