James Kilner - selected references

1 Kilner, J. M. & Friston, K. J. (2014). Relating the "mirrorness" of mirror neurons to their origins. *Behavioral and Brain Sciences, 37,* 207-208.
Notes: Ever since their discovery, mirror neurons have generated much interest and debate. A commonly held view of mirror neuron function is that they transform "visual information into knowledge," thus enabling action understanding and non-verbal social communication between con-specifics (Rizzolatti & Craighero 2004). This functionality is thought to be so important that it has been argued that mirror neurons must be a result of selective pressure

2 Press, C. M. & Kilner, J. M. (2013). The time course of eye movements during action observation reflects sequence learning. *Neuroreport, 24,* 822-826.
Notes: When we observe object-directed actions such as grasping, we make predictive eye movements. However, eye movements are reactive when observing similar actions without objects. This reactivity may reflect a lack of attribution of intention to observed actors when they perform actions without 'goals'. Alternatively, it may simply signal that there is no cue present that has been predictive of the subsequent trajectory in the observer's experience. To test this hypothesis, the present study investigated how the time course of eye movements changes as a function of visual experience of predictable, but arbitrary, actions without objects. Participants observed a point-light display of a model performing sequential finger actions in a serial reaction time task. Eye movements became less reactive across blocks. In addition, participants who exhibited more predictive eye movements subsequently demonstrated greater learning when required either to execute, or to recognize, the sequence. No measures were influenced by whether participants had been instructed that the observed movements were human or lever generated. The present data indicate that eye movements when observing actions without objects reflect the extent to which the trajectory can be predicted through experience. The findings are discussed with reference to the implications for the mechanisms supporting perception of actions both with and without objects as well as those mediating inanimate object processing

3 Press, C., Weiskopf, N., & Kilner, J. M. (2012). Dissociable roles of human inferior frontal gyrus during action execution and observation. *NeuroImage, 60,* 1671-1677.
Notes: There has been recent controversy about whether activation in the human inferior frontal gyrus (IFG) and Brodmann Area (BA) 6 when observing actions indicates operation of mirror neurons. Recent functional magnetic resonance imaging (fMRI) data have demonstrated repetition suppression (RS) effects in posterior IFG which are consistent with the presence of mirror neurons in humans. Here we investigated whether there were similar RS

effects elsewhere in the IFG and BA6, or whether, instead, activation in other locations may signal operation of alternative mechanisms. Replicating previous findings, we found RS effects in posterior IFG consistent with the operation of mirror neurons. However, these effects were not found in other locations in IFG and BA6. Additionally, activation patterns in anterior regions of IFG suggested dissociable operations when observing and executing actions. Therefore, caution should be exercised when claiming that activations in many locations during action observation indicate the operation of mirror neurons. Activation may instead reflect alternative mechanisms, such as encoding of the semantic features of actions

4 Kilner, J. M. (2011). More than one pathway to action understanding. *Trends in Cognitive Sciences, 15,* 352-357.
Notes: Many believe that the ability to understand the actions of others is made possible by mirror neurons and a network of brain areas known as the action-observation network (AON). Despite nearly two decades of research into mirror neurons and the AON, however, there is little evidence that they enable the inference of the intention of observed actions. Instead, theories of action selection during action execution indicate that a ventral pathway, linking middle temporal gyrus with the anterior inferior frontal gyrus, might encode these abstract features during action observation. Here I propose that action understanding requires more than merely the AON, and might be achieved through interactions between a ventral pathway and the dorsal AON
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5 Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience, 29,* 10153-10159.
Notes: There is much current debate about the existence of mirror neurons in humans. To identify mirror neurons in the inferior frontal gyrus (IFG) of humans, we used a repetition suppression paradigm while measuring neural activity with functional magnetic resonance imaging. Subjects either executed or observed a series of actions. Here we show that in the IFG, responses were suppressed both when an executed action was followed by the same rather than a different observed action and when an observed action was followed by the same rather than a different executed action. This pattern of responses is consistent with that predicted by mirror neurons and is evidence of mirror neurons in the human IFG
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6 Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). The mirror-neuron system: a Bayesian perspective. *Neuroreport, 18,* 619-623.
Is it possible to understand the intentions of other people by simply observing their movements? Many neuroscientists believe that this ability depends on the

brain's mirror-neuron system, which provides a direct link between action and observation. Precisely how intentions can be inferred through movement-observation, however, has provoked much debate. One problem in inferring the cause of an observed action, is that the problem is ill-posed because identical movements can be made when performing different actions with different goals. Here we suggest that this problem is solved by the mirror-neuron system using predictive coding on the basis of a statistical approach known as empirical Bayesian inference. This means that the most likely cause of an observed movement can be inferred by minimizing the prediction error at all cortical levels that are engaged during movement observation. This account identifies a precise role for the mirror-neuron system in our ability to infer intentions from observed movement and outlines possible computational mechanisms