

---

# Observing and Learning Complex Actions: On the Example of Guitar Playing

Tom Gardner and Emily S. Cross

---

## Abstract

With very little effort or thought, we can understand the goals and intentions of other people we encounter in our daily lives through watching their movements. In this chapter, we discuss the action observation network (AON), which is thought to be a key player in linking action perception, production, and understanding. We focus on two prominent theories of AON function and detail how different kinds of experience (namely, physical and visual experience) shape AON engagement. We then highlight work done by our laboratory and others that uses complex guitar and dance training paradigms to trace the emergence of experience-dependent plasticity in the human brain and behavior. This work highlights common and distinct neural signatures of visual and visuomotor learning and how such training paradigms can help to adjudicate between competing theories of AON function. The use of cutting edge methodological techniques is also evaluated, and we conclude with some considerations of implications for musicians and dancers and future directions for this research.

---

## Keywords

Predictive coding • Action observation • AON • Direct matching • Familiarity • Physical learning • Visual learning • Dance • Music • Guitar • Expertise

## Contents

|   |   |
|---|---|
| Introduction .....  | 2 |
| State of the Art .....  | 3 |
| Theoretical Perspectives on Linking Action and Perception ..... | 3 |
| Insights from Physical Practice/Physical Familiarity .....      | 5 |
| Insights from Visual Experience/Visual Familiarity .....        | 7 |

---

T. Gardner • E.S. Cross  
Bangor University, Bangor, North Wales, UK  
e-mail: [e.cross@bangor.ac.uk](mailto:e.cross@bangor.ac.uk)

---

|   |    |
|---|----|
| Methodological Considerations for Advancing Understanding of Action Cognition ..... | 9  |
| Conclusions .....   | 10 |
| Cross-References .....  | 11 |
| References .....  | 11 |

---

## Introduction

Humans are a highly social species who are in near-constant visual contact with conspecifics. When we observe others moving around us, we are able to make many rich inferences about these individuals' goals, intentions, and desires. For example, if sitting in a café and observing a friend reach to grasp her coffee cup, from this action, we might infer that our friend is thirsty, or wishes to get warm by imbibing a hot beverage, or perhaps is hoping a dose of caffeine will help to wake her (Hamilton and Grafton 2006; Hamilton 2013; Ramsey and Hamilton 2010). The goal of her reaching action would be to grasp the coffee cup, with the intention of lifting it up to take a drink from it. Integral to this concept is that we actively predict the actions as they unfold, allowing us to rapidly update our predictions of subsequent actions in an online fashion (Blakemore and Frith 2005; Falck-Ytter et al. 2006). If, for example, our friend in the café appears to reach for her coffee cup but deviates toward the sugar, our understanding of her intention must change, no longer is her goal to grasp the coffee cup.

The ability to obtain such rich information from others' actions likely stems from a particular type of neuron first identified within the nonhuman primate brain: so-called mirror neurons. These neurons were found to respond both when monkeys observed or executed the same or similar arm movements (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996). These seminal findings performed with nonhuman primates lend support to the notion that observed and executed actions might share some manner of higher order action representation within the same neural tissue (Gallese and Goldman 1998; Rizzolatti et al. 2001). Returning to the example used previously, when observing our friend reaching for her coffee cup, one can extrapolate the goal and intention of the friend's action by simulating this same action within one's own motor system. It is this *shared representation* that allows us, as observers, to both understand as well as learn new actions. However, it is important to note the findings described above relating to mirror neurons responding in a similar manner to observed and executed actions all came from investigations performed within the macaque brain. The fine-scale precision for measuring neuronal response from individual neurons is difficult to achieve in human participants, as single unit or neural population recordings in humans are only possible in rare and specialized neurosurgery contexts. However, a growing corpus of studies using human neuroimaging approaches, such as functional magnetic resonance imaging (fMRI), offers compelling evidence that similar neural mechanisms are at play within the human brain. For example, Kilner et al. (2009) used a repetition suppression paradigm, where repeated presentation of a particular stimulus or feature results in reduced activity in a particular brain region of interest, to demonstrate a pattern of

activity within inferior frontal gyrus that is consistent with the monkey mirror neuron findings. The question of whether individual mirror neurons actually exist in the human brain remains to be definitively answered by future work, yet accruing evidence suggests that *some* degree of correspondence clearly exists between executed and observed actions within the human brain.

In this chapter, we examine the main theoretical perspectives that underpin work in this domain before presenting in more depth how research exploring the impact of physical experience and visual experience helps shape our understanding of shared representations between action and perception. Throughout each section, we highlight work from our own laboratory that combines complex dance or guitar learning paradigms with brain imaging. Finally, we consider the value of combining sophisticated training interventions with cutting edge neuroimaging approaches to further advance our understanding of experience-dependent plasticity in the AON.

---

## State of the Art

Since the discovery of mirror neurons in the nonhuman primate brain, research performed with human participants over the past two decades demonstrates an extensive network of sensorimotor cortical regions that are involved in action perception and production termed the action observation network (AON) (Cross et al. 2009b; Grafton 2009; Keysers and Gazzola 2009; Caspers et al. 2010). Unlike the mirror neurons first discovered in the monkey brain, the AON does not require as close a correspondence between observed and executed actions but is instead more broadly engaged when we observe others in action (Iacoboni et al. 2001; Gallese et al. 2004; Schippers and Keysers 2011). It has been suggested that together, the brain regions composing this network help us to understand, reproduce, and learn from others' actions (Gallese et al. 2004; Schippers and Keysers 2011). However, many open questions remain concerning the extent to which an individual's prior experience with an observed action might shape engagement of this network and subsequent learning or understanding of others' actions. Through careful exploration of this topic, we can uncover valuable insights into how we are able to transform visual information into sophisticated motor acts, an ability that is particularly pronounced in expert dancers and musicians.

---

## Theoretical Perspectives on Linking Action and Perception

Two prominent theories of action understanding have been proposed and extensively debated. Both models provide strong predictions about how fluctuations in an observer's familiarity with an observed action might shape engagement of the core nodes that compose the AON. The first model, known as the direct matching hypothesis of action understanding (Rizzolatti et al. 2001; Gallese and Goldman 1998; Wolpert et al. 2003; Umiltà et al. 2001; Kohler et al. 2002), suggests that an action's meaning is understood via the AON, supporting simulation of an observed

action by matching the goal or intention of what that movement would be if performed by the observer. This model shares many parallels with the “like me” hypothesis (Meltzoff 2007), which states that if an action or actor is more “like me,” we would expect greater engagement of sensorimotor mechanisms that support action observation and execution (i.e., the AON). Returning to the coffee cup example introduced earlier, we can relate to this action because we have likely performed it many times ourselves, and thus we should be able to understand the action in terms of the actor’s goals and intentions by using our own prior experience. This use of experience-driven simulation mechanisms (Sinigaglia 2013) in understanding an action forms the foundations of the direct matching hypothesis.

In terms of the mechanism that enables the direct matching hypothesis to support action understanding, by use of forward models (Wolpert et al. 2003), the visual information of an observed action first enters the network through higher order visual areas. This information then flows anteriorly through the AON, eventually arriving at motor and premotor cortices. Engagement of the motor system enables an observer to understand how the action should unfold and thus supports an observer in reading the intentions and goals of an observed actor.

One criticism of this hypothesis is based on the name itself; *direct* matching. As noted by Csibra (1993), multiple means can be taken in order to obtain an individual goal. For example, one can drink from a mug by either raising the mug to one’s face or lowering one’s face to the mug; the goal to drink remains the same. Thus, the direct matching implied by this hypothesis must remain resilient to the different means by which one might achieve a specific action goal. As such, the ability must be present to observe an action, map it onto one’s own motor system, and from there form a *higher-order action understanding*. This point was addressed by the authors of the original model (Rizzolatti and Sinigaglia 2010) in an extension that is termed the goal-mirroring model (Steinhorst and Funke 2014). In this variation, the authors propose that intention can be gauged by matching the goal of the observed action to an internal motor act with the same goal, regardless of whether the kinematics precisely match.

When we observe a familiar action, the direct matching hypothesis has a clear explanation for how the AON responds. As one’s experience or familiarity with an observed actions increase, the AON’s simulation of how that action might unfold over time becomes more accurate and resonance between an observer’s motor system and an observed action is maximized (c.f., Calvo-Merino et al. 2005; Cross et al. 2006). However, such an account would struggle to explain how the AON would process an *unfamiliar* action that is *not* in the observer’s repertoire. We now know from a number of studies that not only is the AON engaged when viewing such unfamiliar actions (Cross et al. 2009a; Ramsey and Hamilton 2010), but some evidence suggests that in certain situations, the AON can even show *stronger* engagement to unfamiliar compared to familiar actions (Cross et al. 2012, 2013). Therefore, the direct matching hypothesis provides a partial but incomplete explanation for the role of familiarity within the AON but stops short of being able to explain why in some situations unfamiliar actions can drive the AON more strong

than familiar actions. This fuels a need to further understand the interplay between experience, familiarity, and the AON's role in action understanding.

A model that extends the premise of the direct matching hypothesis is the predictive coding account. Predictive coding models of AON function (Keysers and Perrett 2004; Kilner et al. 2007a, b; Gazzola and Keysers 2009; Schippers and Keysers 2011) are predicated on the use of perceptuomotor maps to predict and interpret observed actions (Lamm et al. 2007; Schubotz 2007; Urgesi et al. 2010). Such models have the potential to help resolve seemingly discrepant findings concerning the relationship between familiarity of an observed movement and engagement of sensorimotor cortices.

The predictive coding framework proposes a Bayesian comparison of predicted and observed actions via use of forward and inverse models and comprises a reciprocally modulated network of premotor, inferior parietal and posterior temporal cortices. Activity within this network aims to minimize the differences between observed and predicted actions. When observing a less familiar action, predictions (feedback) are lacking or are under-informed and thus do not match the observed actions (feedforward), which equates to high prediction error. This should manifest as increased AON engagement for highly *unfamiliar* actions, as the influence of feedforward/perceptual activity is heavily relied upon. When viewing an action that is familiar, however, the predictions generated by the network are more precise and thus minimize prediction error. The minimizing of prediction error can also manifest as increased AON engagement, as predictions projected posteriorly are stronger than when prediction error was higher during unfamiliar action observation. The reciprocal nature of this framework allows for the explanation of robust AON engagement for both familiar *and* unfamiliar actions and relatively decreased AON engagement for actions that are neither highly unfamiliar nor familiar.

Both the direct matching and predictive coding hypotheses remain prominent models of action understanding. These two accounts both rely on forward models and higher order representations of actions, while the predictive coding account's inclusion of inverse models enables comparisons between observed and predicted actions. When we apply the question of familiarity to these models, the direct matching hypothesis cannot fully explain the findings in the literature of strong AON engagement when observing highly familiar *or* highly unfamiliar actions, depending on the experimental context. In contrast, a predictive coding account has potential to explain these discrepant findings, yet requires additional examination and empirical support.

---

## Insights from Physical Practice/Physical Familiarity

One avenue by which we can explore how experience shapes links between action and perception within the human brain involves documenting brain changes that occur in concert with the acquisition of physical experience with a particular action or set of actions. Along these lines, Basler et al. (2014) showed expert tennis players

and expert volleyball players tennis and volleyball serves while these individuals underwent fMRI. This design allowed for an intriguing comparison as each group was an expert in one sport and a novice in the other. These researchers found that when expert athletes observed serves for their non-expert sport (i.e., tennis players observing volleyball serves or volleyball players observing tennis serves), greater activity emerged within the AON than when these same individuals observed serves being made in their own expert sport. This finding challenges the assumptions made by the direct matching hypothesis and suggests that familiarity and AON engagement likely do not share a linear, positive relationship.

Researchers in this field have also investigated how physical practice changes AON activity with more complex tasks, such as guitar playing. While the physical skills displayed by professional guitarists are impressive to watch (and listen to), the micro-actions involved in playing the guitar are relatively easy (depressing the fingers against particular frets while plucking one or several strings). However, the combination of coordinating the fingers of one hand to press individual strings in specific locations in a particular sequence at precisely the right time while ensuring the other hand is strumming or plucking in the right place at the right time makes the task of playing the guitar quite challenging for novices to learn. Therefore, guitar playing tasks can be ideal for assessing how training or new motor learning influences brain activity. It should be noted, however, that actually playing a guitar in the confines of an fMRI scanner makes the use of a whole guitar difficult (though not impossible; see below), so some studies have broken down guitar playing into simpler components (for example, focusing just on forming chords with one hand on a simplified guitar neck). Moreover, it should also be noted that cognitive neuroscientific investigations of guitar learning most often focused on the most basic manual gestures required to depress and pluck strings and thus cannot offer the same multidimensional analysis of guitar playing that more sophisticated studies involving motion capture and analysis of audio and musical score can (c.f., Perez-Carrillo et al. 2016).

In one of the first cognitive neuroscientific studies into the neural bases of imitation learning that used guitar playing, Buccino et al. (2004) scanned guitar novices using fMRI, while participants observed and executed guitar chords. The primary finding reported by this study was that when observing the chord playing actions of an expert with the intention to later imitate these same chords, strong activation of the AON emerged. Subsequent work by the same group of researchers tested the effects of training participants on the guitar chords (Vogt et al. 2007). The findings from this study demonstrated that unpracticed actions elicited greater engagement of the AON compared to practiced actions. Together, these findings indicate that the AON is more active when an action is not yet physically familiar to the observer (and the observer is thought to be trying to learn the observed action).

As mentioned above, the concept of using a fully functional guitar within the scanner is difficult to achieve, thus the above studies referenced above have used just the neck of the guitar. Recently, however, we created a fully functioning bass guitar that was compatible with fMRI. By using materials to build a guitar that were safe to use within the strong magnetic field of the fMRI scanner, we were able to examine

both the observation and execution of complex guitar playing actions before and after an intensive training intervention (Gardner et al. 2017). For this study, we asked guitar novices to play along with segments of popular songs in a video game environment while undergoing functional neuroimaging. Participants were then invited to the lab where they practiced playing the songs in a similar setting to that of the fMRI scanner (i.e., supine, in the video game environment; see Fig. 1). After 3 days of training, the participants were invited back to undergo a second fMRI scanning session, allowing us to evaluate the effects of training action execution. Furthermore, we aimed to directly assess the predictions of the prominent action understanding models (direct matching and predictive coding). By assessing activity within individual regions of the AON that responded to action observation and execution, we then fitted different models (linear and nonlinear) to the data. Our findings revealed that the relationship between familiarity and activity within core AON regions was nonlinear, thus further challenging the direct matching account of AON function and providing more evidence in support of the predictive coding model (Gardner et al. 2017).

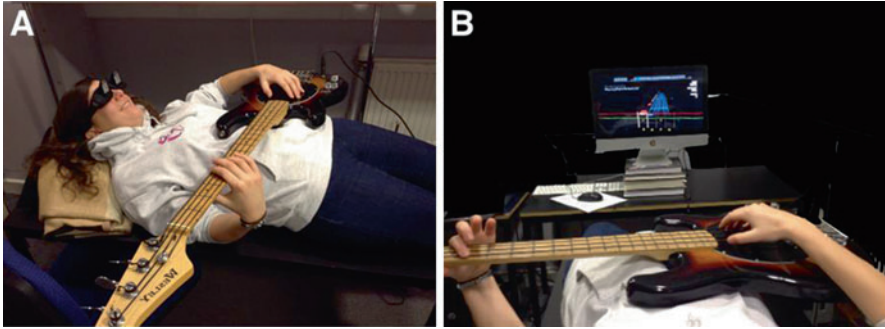
---

## Insights from Visual Experience/Visual Familiarity

While testing the impact of physical experience can help us to delineate AON functions and mechanisms in more detail, examining *visual* experience (either alone or in conjunction with physical experience) can illuminate additional features about the action-perception relationship and how experience changes this relationship. Schippers and Keysers (2011) aimed to test the flow of information between brain regions that respond to the execution and observation of actions. In this study, the researchers used simple hand gestures to test the predictions of predictive coding models and found greater feedback modulations when the gestures were more familiar to the participants. This suggests that when using visual exposure as the measure of familiarity, there are similar findings to when physical practice is used.

This conclusion was further supported by Gardner et al. (2017) in their guitar learning study. As well as using physical practice within the training paradigm, participants also took part in a visual training condition wherein they observed a distinct set of guitar sequences to those they physically trained on being played by an expert guitar player both in the scanner and over the training period. Using the same region of interest analysis approach where the response within individual AON regions is fit to linear and nonlinear models, the authors showed that across all regions, the model that best explained the relationship between visual familiarity and activity was also nonlinear in nature. Furthermore, the authors also tested participants' ability to physically perform songs that they visually trained on after the second scanning session. Here they demonstrated that training by visual exposure alone significantly improved performance compared to songs which remained untrained.

Another rich variety of motion stimulus that has proved valuable for investigating mechanisms and theoretical perspectives of AON function in the visual domain are



**Fig. 1.** (a) View of participant practicing guitar during training – third person perspective. (b) Participant’s view of guitar and game play during training – first person perspective.

the complex whole body movements involved in dance. Similar to the guitar playing examples described above, many of the basic building blocks for movements we see performed by expert dancers are executable by most people. However, the timing, precision, and scale of these same basic movements when performed by expert dancers make these actions much more complex and difficult for novices to reliably reproduce. Moreover, some actions can be readily understood in terms of kinematics and intentions, but the observer might not be able to perform the action (e.g., not all of us can execute a triple spin on one leg, yet we can understand how one *might* perform this action). Using dance movements, Cross et al. (2012) demonstrated stronger AON engagement when participants observed less familiar dance movements compared to more familiar ones. Furthermore, Gardner et al. (2015) used a similar set of dance movements that ranged between extremely familiar and extremely unfamiliar and asked participants to rate how physically familiar they were with each movement. Using participants’ ratings as parametric modulators in the brain imaging design, the authors showed a positive relationship between familiarity ratings and the amplitude of neural engagement within core AON regions. Clearly, as is highlighted by these two examples from our own laboratory, findings from this literature are far from consistent concerning the relationship between the amplitude of AON response and participants’ objective or subjective familiarity ratings. One conclusion that we are reasonably confident in stating, however, is that the relationship between AON engagement and familiarity/experience certainly appears to be nonlinear in nature. This suggestion is more in line with a predictive coding model of action understanding compared to a direct matching model. To probe this claim, Gardner et al. (2015) combined participants’ subjective ratings of movement familiarity with effective connectivity to explore changes in the coupling between core AON regions as participants’ ratings of familiarity for observed dance videos varied. Using dynamic causal modelling (Friston et al. 2003), they showed that as familiarity ratings increase, the connectivity between posterior regions of the AON (namely, the middle temporal gyrus and the inferior parietal lobule) attenuates or dampens. The authors concluded that this finding



provides partial support for the predictive coding account, as it did not fully support predictions made by this account in terms of the role of varying degrees of familiarity on connectivity between AON regions. However, the data were consistent with the notion that increased familiarity results in a decrease of the influence of perception-focused regions of the AON (see Gardner et al. 2015 for further discussion of this issue). Indeed, follow-up work by Gardner and Cross (in preparation), again using the guitar learning paradigm, suggests that more concrete measures of learning and physical ability (and by extension, familiarity), such as guitar playing aptitude, can allow us to probe the predictive coding model of AON function in more depth.

Finally, a recent study by Kirsch and Cross (2015) demonstrated that layering different kinds of sensorimotor experience (visual, auditory, and physical) when novice dancers learn new dance sequences appears to have an additive value in terms of AON engagement. In other words, the more modalities through which one learns a new action sequence, the more value it provides to the trainee in terms of both behavioral performance and amplitude of AON response. This latter point is relevant as this study also reported a positive correlation between individual participants' performance aptitude and the magnitude of response within the left premotor and intraparietal cortices, two core AON regions, when participants observed dance sequences they had physically practiced or those that they had simply observed (Kirsch and Cross 2015). Taken together, the findings discussed in this section suggest that visual experience can also instill new action learning, even in complex learning paradigms that involve guitar playing or dancing. Moreover, work from our lab and other groups is continuing to delineate how the AON is shaped by visual and physical experience, thus opening many rich opportunities to design novel learning or rehabilitation programs that focus on building physical abilities via visual experience.

---

## **Methodological Considerations for Advancing Understanding of Action Cognition**

So far, we have discussed two prominent theories of action understanding and a selection of studies that have used visual and physical experience to test the nature of the mechanisms involved in the execution and observation of actions. A powerful methodological approach available to research in controlling levels of familiarity is the use of a training paradigm.

Training paradigms offer researchers the ability to systematically control levels of familiarity participants have with stimuli. Effects of learning can be methodically tested, and the experimenters maintain control over the amount and type of exposure individual participants have with action stimuli. However, training approaches are also not without their drawbacks, as they can be extremely time consuming for both researcher and participant. Requiring participants to attend multiple sessions can be challenging not just in terms of participant attrition but also the repetition of stimuli exposure (visual or physical) can lead to boredom for the participant, which can in turn skew the results and/or obscure the true nature of the behavior or learning

process. Keeping these limitations in mind, training paradigms nonetheless serve as a valuable approach for examining experience-dependent plasticity in the human brain and behavior.

The growing array of methods and analytical approaches available allow for activity within the brain to be examined without the need for invasive measures. Although neuroimaging facilities are expensive to establish and maintain, their use is by now widespread and offers a valuable approach for exploring the neural underpinnings of (some) cognitive and behavioral processes. However, neuroimaging technology is only as valuable as the questions asked and the design used. An emerging trend in cognitive neuroscience is seeing researchers increasingly moving away from magnitude-based approaches for neuroimaging studies and toward sophisticated multivariate analytical approaches. For example, comparing the activity within certain brain regions before and after training might tell us how these brain regions respond in a very general sense based on a specific training intervention, but such comparisons tell us little about how these regions might be *interacting*. As alluded to in the discussion of models of action understanding earlier in this chapter, the flow of information between core AON regions will be important to understand if we are to better comprehend how the brain processes and extracts information from others' movements. Connectivity measures, like those used in the studies discussed previously, allow for this information exchange between brain regions to be tapped into. By using connectivity approaches coupled with training paradigms, the interplay between core sensorimotor regions of the AON can be assessed more precisely, as can the influence of variations in experience or familiarity. Thus, these emerging methodological approaches should enable us to better unpick and evaluate the leading theoretical perspectives concerning the relationship between sensorimotor experience, action learning, and perception.

---

## Conclusions

In conclusion, combining noninvasive functional neuroimaging approaches with complex skill-learning paradigms, such as those that involve learning to play the guitar or dance, can illuminate fundamental features of the interplay between action and perception in the human brain and how experience modulates this relationship. Two prominent models of action understanding have been proposed that attempt to explain how ongoing visual or visuomotor experience shape perception and a wealth of literature exists that explores this issue. Such studies have focused on a variety of actions, ranging from simple button pressing tasks all the way to complex music and dance tasks. In our laboratory, we have focused on the more complex end of the action spectrum, combining multi-day training paradigms where novice participants acquire music or dance experience with pre- and post-functional neuroimaging measures and univariate and multivariate analyses. By applying such approaches to address the underlying relationship between familiarity and AON activity, this opens up exciting new avenues for further research as we begin to understand the brain as a (more) fully interconnected network of regions, rather than isolated

snapshots of the properties of single brain regions. In addition, this research also has the potential to inform novice music or dance learners, as well as professionals in these fields, as we further our understanding of the impact and benefit of visual experience on new action learning.

---

## Cross-References

- ▶ [3D Dynamic Pose Estimation Using Reflective Markers or Electromagnetic Sensors](#)
- ▶ [3D Musculoskeletal Kinematics Using Dynamic MRI](#)
- ▶ [Optimal Control Strategies for Human Movement](#)
- ▶ [Perceptual Evaluation of Human Animation](#)

---

## References

- Basler N, Lorey B, Pilgramm S, Naumann T, Kindermann S, Stark F, Zentgraf R, Williams AM, Munzert J (2014) The influence of expertise on brain activation of the action observation network during anticipation of tennis and volleyball serves. *Front Hum Neurosci* 8:586
- Blakemore SJ, Frith C (2005) The role of motor contagion in the prediction of action. *Neuropsychology* 43:260–267
- Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund H-J, Rizzolatti G (2004) Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron* 42:323–334
- Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P (2005) Action observation and acquired motor skills: an fMRI study with expert dancers. *Cereb Cortex* 15:1243–1249
- Caspers S, Zilles K, Laird A, Eickhoff S (2010) ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage* 50:1148–1167
- Cross ES, Hamilton AF, Grafton ST (2006) Building a motor simulation de novo: observation of dance by dancers. *NeuroImage* 31(3):1257–1267
- Cross ES, Hamilton AF, Kraemer DJ, Kelley WM, Grafton ST (2009a) Dissociable substrates for body motion and physical experience in the human action observation network. *Eur J Neurosci* 30(7):1383–1392
- Cross ES, Kraemer DJ, Hamilton AF, Kelley WM, Grafton ST (2009b) Sensitivity of the action observation network to physical and observational learning. *Cereb Cortex* 19(2):315–326
- Cross ES, Liepelt R, de C. Hamilton AF, Parkinson J, Ramsey R, Stadler W, Prinz W (2012) Robotic movement preferentially engages the action observation network. *Hum Brain Mapp* 33(9):2238–2254
- Cross ES, Stadler W, Parkinson J, Schütz-Bosbach S, Prinz W (2013) The influence of visual training on predicting complex action sequences. *Hum Brain Mapp* 34:467–486
- Csibra G (1993) Action mirroring and action understanding: an alternative account. In: Haggard P, Rossetti Y, Kawato M (eds) *Sensorimotor foundations of higher cognition*. Oxford University Press, Oxford, pp 435–459
- di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G (1992) Understanding motor events: a neurophysiological study. *Exp Brain Res* 91(1):176–180
- Falck-Ytter T, Gredebäck G, von Hofsten C (2006) Infants predict other people's action goals. *Nat Neurosci* 9:878–879
- Friston KJ, Harrison L, Penny WD (2003) Dynamic causal modelling. *NeuroImage* 19:1273–1302
- Gallese V, Goldman AI (1998) Mirror neurons and the simulation theory of mind reading. *Trends Cogn Sci* 2:493–501

- Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119(Pt 2):593–609
- Gallese V, Keysers C, Rizzolatti G (2004) A unifying view of the basis of social cognition. *Trends Cogn Sci* 8(9):396–403
- Gardner T, Goulden N, Cross ES (2015) Dynamic modulation of the action observation network by movement familiarity. *J Neurosci* 35(4):1561–1572
- Gardner T, Aglinskas A, Cross ES (2017). Using guitar learning to probe the Action Observation Network's response to visuomotor familiarity. *NeuroImage*, 157:174–189.
- Gazzola V, Keysers C (2009) The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb Cortex* 19:1239–1255
- Grafton ST (2009) Embodied cognition and the simulation of action to understand others. *Ann N Y Acad Sci* 1156:97–117
- Hamilton AF (2013) The mirror neuron system contributes to social responding. *Cortex* 49(10):2957–2959
- Hamilton AF, Grafton ST (2006) Goal representation in human anterior intraparietal sulcus. *J Neurosci* 26:1133–1137
- Iacoboni M, Koski LM, Brass M, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Rizzolatti G. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the National Academy of Sciences USA*, 98(24):13995–13999.
- Keysers C, Gazzola V (2009) Expanding the mirror: vicarious activity for actions, emotions, and sensations. *Curr Opin Neurobiol* 19:666–671
- Keysers C, Perrett DI (2004) Demystifying social cognition: a Hebbian perspective. *Trends Cogn Sci* 8:501–507
- Kilner JM, Friston KJ, Frith CD (2007a) Predictive coding: an account of the mirror neuron system. *Cogn Process* 8:159–166
- Kilner JM, Friston KJ, Frith CD (2007b) The mirror-neuron system: a Bayesian perspective. *NeuroReport* 18:619–623
- Kilner JM, Neal A, Weiskopf N, Friston KJ, Frith CD (2009) Evidence of mirror neurons in human inferior frontal gyrus. *J Neurosci* 29(32):10153–10159
- Kirsch LP, Cross ES (2015) Additive routes to action learning: layering experience shapes engagement of the action observation network. *Cereb Cortex* 25:4799–4811
- Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G (2002) Hearing sounds understanding actions: action representation in mirror neurons. *Science* 297:846–848
- Lamm C, Nusbaum HC, Meltzoff AN, Decety J (2007) What are you feeling? Using functional magnetic resonance imaging to assess the modulation of sensory and affective responses during empathy for pain. *Brain Res* 1227:153–161
- Meltzoff AN (2007) Like me: a foundation for social cognition. *Dev Sci* 10(1):126–134
- Perez-Carrillo A, Arcos J-L, Wanderley M (2016) Estimation of guitar fingering and plucking controls based on multimodal analysis of motion, audio and musical score. *Lect Notes Comput Sci: Music Mind Embodiment* 9617:71–87
- Ramsey R, Hamilton AFDC (2010) Triangles have goals too: understanding action representation in left aIPS. *Neuropsychologia* 48(9):2773–2776
- Rizzolatti G, Sinigaglia S (2010) The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat Rev Neurosci* 11:264–274
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996) Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res* 3:131–141
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2:661–670
- Schippers MB, Keysers C (2011) Mapping the flow of information within the putative mirror neuron system during gesture observation. *NeuroImage* 57(1):37–44
- Schubotz RI (2007) Prediction of external events with our motor system: towards a new framework. *Trends Cogn Sci* 11:211–218

- Sinigaglia C (2013) What type of action understanding is subserved by mirror neurons? *Neurosci Lett* 540:59–61
- Steinhorst A, Funke J (2014) Mirror neuron activity is no proof for action understanding. *Front Hum Neurosci* 8:333
- Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C et al (2001) I know what you are doing. A neurophysiological study. *Neuron* 31:155–165
- Urgesi C, Maieron M, Avenanti A, Tidoni E, Fabbro F, Aglioti SM (2010) Simulating the future of actions in the human corticospinal system. *Cereb Cortex* 20(11):2511–2521
- Vogt S, Buccino G, Wohlschläger AM, Canessa N, Shah NJ, Zilles K, Eickhoff SB, Freund H, Rizzolatti G, Fink GR (2007) Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. *NeuroImage* 37(4):1371–1383
- Wolpert DM, Doya K, Kawato M (2003) A unifying computational framework for motor control and social interaction. *Philos Trans R Soc Lond Ser B Biol Sci* 358:593–602