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Using guitar learning to probe the Action Observation Network's response to visuomotor familiarity

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ABSTRACT

Watching other people move elicits engagement of a collection of sensorimotor brain regions collectively termed the Action Observation Network (AON). An extensive literature documents more robust AON responses when observing or executing familiar compared to unfamiliar actions, as well as a positive correlation between amplitude of AON response and an observer's familiarity with an observed or executed movement. On the other hand, emerging evidence shows patterns of AON activity counter to these findings, whereby in some circumstances, unfamiliar actions lead to greater AON engagement than familiar actions. In an attempt to reconcile these conflicting findings, some have proposed that the relationship between AON response amplitude and action familiarity is nonlinear in nature. In the present study, we used an elaborate guitar training intervention to probe the relationship between movement familiarity and AON engagement during action execution and action observation tasks. Participants underwent fMRI scanning while executing one set of guitar sequences with a scanner-compatible bass guitar and observing a second set of sequences. Participants then acquired further physical practice or observational experience with half of these stimuli outside the scanner across 3 days. Participants then returned for an identical scanning session, wherein they executed and observed equal numbers of familiar (trained) and unfamiliar (untrained) guitar sequences. Via region of interest analyses, we extracted activity within AON regions engaged during both scanning sessions, and then fit linear, quadratic and cubic regression models to these data. The data best support the cubic regression models, suggesting that the response profile within key sensorimotor brain regions associated with the AON respond to action familiarity in a nonlinear manner. Moreover, by probing the subjective nature of the prediction error signal, we show results consistent with a predictive coding account of AON engagement during action observation and execution that also takes into account effects of changes in neural efficiency.

Introduction

Watching others in action provides important information about other people's goals, intentions, and desires. When we observe others moving around us, we can predict how their current and future actions might unfold, thus enabling us to respond appropriately to those we encounter in a social world (Blakemore and Frith, 2005). Action observation elicits activity in a network of sensorimotor brain regions collectively termed the Action Observation Network (AON; Cross et al., 2009; Grafton, 2009; Keysers and Gazzola, 2009; Caspers et al., 2010). The core brain regions that compose the AON include occipitotemporal regions associated with observing bodies in motion, as well as the premotor cortex and inferior parietal lobule. These latter two brain regions have been shown to contain so-called mirror neurons in the non-human primate brain (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 2001; Umiltà et al., 2001), and demonstrate a similar response profile during action observation and execution in the human brain (Gazzola and Keysers, 2009; for a review see Molenberghs et al., 2012). Previous literature demonstrates that the more familiar an action is, the stronger the response is within these core AON regions (Buccino et al., 2004; Calvo-Merino et al., 2005; Cross et al., 2006; Shimada, 2010). Moreover, we recently demonstrated that complex, whole body movements that participants rated as more familiar were associated with greater AON activity compared to movements rated as less familiar (Gardner et al., 2015). These magnitude-based approaches support experience-driven simulation accounts of action perception (Sinigaglia, 2013), which form the foundation of the direct matching hypothesis of action understanding (Rizzolatti et al., 2001; Gallese and Goldman, 1998; Wolpert et al., 2003; although see Csibra, 2005 and Kilner, 2011 for alternative accounts). In terms of familiarity, a linear relationship between magnitude of AON activity and familiarity would be consistent with this hypothesis: as familiarity increases, the

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simulation of how an action might unfold over time becomes more accurate and resonance between an observer's motor system and an observed action is maximised. This relationship is illustrated in Fig. 1***A***.

On the other hand, an increasing number of studies report findings demonstrating that AON activity does not necessarily follow this linear trend of increasing engagement with increasing familiarity (Gazzola et al., 2007; Liew et al., 2013; Cross et al., 2012; Tipper et al., 2015). These studies demonstrate equivalent or greater AON activity when participants observe actions that are *unfamiliar* (compared to more familiar actions), a finding that appears at odds with a simulation-based account of AON function. The findings from these studies suggest that a linear relationship between AON activity and familiarity is likely too simplistic. In terms of the direct matching hypothesis, this theory would struggle to explain why an unfamiliar action that is *not* in the observer's repertoire would elicit greater AON activity compared to a familiar action. Aspects of predictive coding models of AON function (Keysers and Perrett, 2004; Kilner et al., 2007a, 2007b; Gazzola and Keysers, 2009; Schippers and Keysers, 2011; Tipper et al., 2015), predicated on the use of perceptuomotor maps to predict and interpret observed actions (Lamm et al., 2007; Schubotz, 2007; Urgesi et al., 2010) may help resolve these seemingly discrepant findings concerning the relationship between action familiarity and engagement of sensorimotor cortices. This framework proposes a Bayesian comparison of predicted and observed actions, creating a reciprocally modulated network comprising premotor cortex (including the inferior frontal gyrus), inferior parietal lobule, and posterior temporal cortices (middle and superior temporal gyri). Activity in this network serves to minimise differences between observed and predicted actions. When observing a less familiar action, predictions (feedback signals from frontal → parietal → temporal cortices) are lacking or are under informed, and thus do not match incoming information about the observed action (feedforward signals from temporal → parietal → frontal cortices), which equates to high prediction error. This could result in robust AON engagement for highly unfamiliar actions, as the influence of feedforward/perceptual activity is heavily relied upon. When viewing an action that is highly familiar, however, predictions generated by the network should be much more precise, thus minimising prediction error. The minimising of prediction error could also manifest as robust AON engagement, this time due to the strength of feedback signals projecting posteriorly (which were weaker when movements were unfamiliar and prediction error was higher; see also Cross et al., 2012). The reciprocal nature of exchanging prediction error signals between core AON nodes allows for the explanation of robust AON engagement for both familiar *or* unfamiliar actions, relative to actions of an intermediate level of familiarity (illustrated in Fig. 1*B* [1]). It is important to note as well that while this Bayesian framework has been most fully developed in the realm of action observation, it also has been applied to action execution, formally known as active inference (Friston, 2005).

As several authors have now suggested, a predictive coding account of action familiarity and AON engagement could manifest as a quadratic, or U-shaped, function (Cross et al., 2012; Liew et al., 2013). However, as identified within the predictive coding literature (Kilner et al., 2007a, 2007b; Friston, 2005), a system that relies on Bayesian comparisons would need to continually update predicted movements in relation to actual movements. For example, when observing an expert guitarist playing a scale (a familiar sequence of actions for both novice and expert guitarists), the player may use all her fingers to achieve this goal. As such, the actions performed by an expert guitarist to play a scale might look much different to those performed by a novice guitarist to play the same scale (i.e., a novice might use fewer fingers and/or transition between notes more awkwardly), even though the musical outcome (playing a scale) remains the same. Therefore, the ability to predict others' actions is subject to continual evaluation, and, at times, reassessment of predictions (c.f. Shadmehr and Holcomb, 1997). A quadratic function may thus not fully capture the dynamic nature of learning, prediction, and experience-driven changes in AON engagement. When considering a quadratic framing of the AON engagement and familiarity relationship, a question remains concerning what happens to AON engagement during the trough of the curve. One possibility is that ongoing evaluation of predicted and actual actions manifests as local reductions in activity within a testing session due to practice, in line with Neural Efficiency (NE) effects (Babiloni et al., 2010; Kelly and Garavan, 2005; Wiestler and Diedrichsen, 2013). In keeping with this prior work on neural efficiency, we might expect that reduced activity within a testing session should recover during subsequent testing sessions, and then reduce again as familiarity and experience continue to accrue. This conceptualisation, combining the predictive coding theoretical account with notions of neural efficiency, would create a cubic shaped response of AON engagement. To our knowledge, these three framings of the relationship between familiarity and AON engagement (i.e., direct matching vs. predictive coding vs. predictive coding + neural efficiency) have not yet been directly compared with empirical evidence.

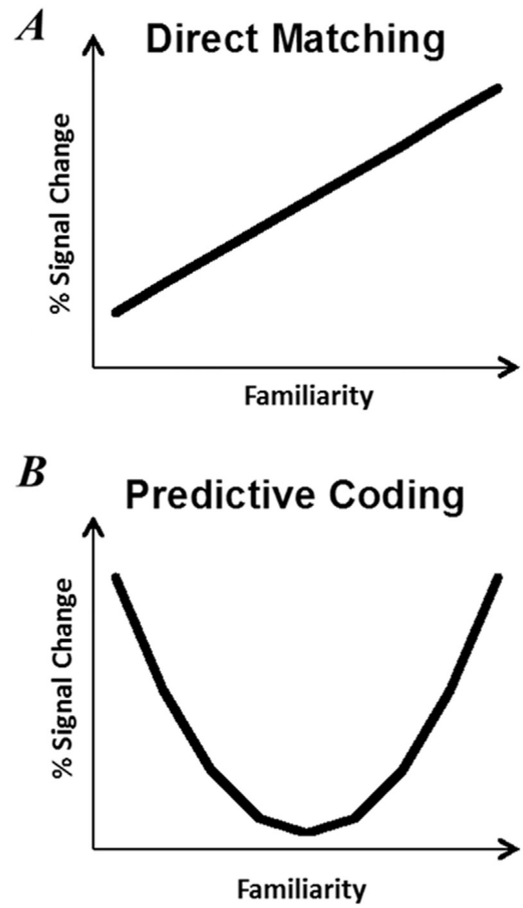

Fig. 1. Hypothesised relationships between familiarity and % signal change (BOLD signal) for both ***A*** direct matching (as proposed by Rizzolatti et al., 2001; Gallese and Goldman, 1998) and ***B*** predictive coding (as proposed by Cross et al., 2012; Liew et al., 2013).

[1] It should be clearly noted, however, that the predictive coding account is much broader in scope in terms of feed-forward and feedback exchange of information between and within networks engaged in action observation and action execution than the experimental approach and resolution of the current study can satisfactorily address (e.g., Keysers and Perrett, 2004; Keysers and Gazzola, 2009; Kilner, 2011). Ongoing work in our laboratory seeks to use effective connectivity measures to explore Hebbian learning and these broader predictive coding ideas in more depth, while the present study is focused on evaluating magnitude-based hypotheses AON engagement that have their origins in distinct theoretical accounts.