Karlinsky, A., Zentgraf, K., & Hodges, N. J. (2017). Action-skilled observation: Issues for the study of sport expertise and the brain. *Progress in brain research*, *234*, 263-289.

https://www.sciencedirect.com/science/article/pii/S0079612317301103?casa_token=SW2QaflvlvgAAAAA:rHIPyhJJOlzg8dT85yzwrvrT-6_xazehkJv2kJ6jSRHIJgWt3gyuRbMYej6ka5geNTPwVxK_w4o

10.1016/bs.pbr.2017.08.009

PREPRINT VERSION

Action-skilled observation: Issues for the study of sport-expertise and the brain

April Karlinsky[1]

Karen Zentgraf[2]

Nicola J. Hodges[1,3]

[1]University of British Columbia

[2]University of Muenster, Germany

1,3 (contact author)

School of Kinesiology

University of British Columbia

Vancouver, BC, Canada

Email: nicola.hodges@ubc.ca

Fax: 1-604-822-6842

Abstract

With a growing body of research devoted to uncovering regions of the brain implicated in action observation following various action-related experiences, including sport, we ask what we know from this research, and what we still need to know, as it pertains to sport and the brain. To do this, we review and integrate knowledge garnered from developmental work, short-term motor learning studies and most significantly from sport athletes across varying skill levels. We consider various neurophysiological methods, including TMS, fMRI and EEG, which have been used to help uncover brain regions involved in action-skilled observation. We are particularly interested in how these processes are related to action prediction and the detection of deceptive actions among athlete groups. This research is considered within broad theoretical frameworks related to action-simulation and prediction, although our main focus is on the brain regions that have been implicated in skilled action observation and the implications of this research for knowledge and further study of sport expertise.

Action-Skilled Observation: Issues for the Study of Sport-Expertise and the Brain

Sports provide an interesting arena to study action experience effects on behavioural outcomes as well as mechanisms and processes that mediate or might explain these outcomes. In many sports, visual-motor experiences are closely tied to performance and in some instances, these experiences can be separated through comparisons of novices, experts, fans or coaches. Action experiences cover a whole range of aspects such as body-related adaptations, visual familiarity, generation of sensorimotor associations, as well as statistical knowledge about the occurrence of events. Of interest in the sports’ expertise domain has been the cortical (and subcortical) activations that accompany or change with sport-training and expertise and the relevance of these for current and future performance, decision making, training and transfer. Here, we review how action experiences modulate observation, with reference to these neurophysiological changes. We refer to this phenomenon as “action-skilled observation”, that is, observation characterized by neural processes associated with motor capabilities. Our aim is to bring together disparate lines of research that speak to skilled perception and inform our understanding of processes underpinning action-skilled observation in sport. We first present an overview of the presumed cortical processes involved in action-observation, specifically those implicated in the action observation network (AON). We then provide a selective review of relevant research pertaining to the emergence of action-skilled observation through normal motor development and short-term motor learning. The main focus of our review is on expert athletes in sports and research showing brain regions that distinguish across skill. We consider the functional relevance of these differences with respect to anticipatory decisions and detection of fakes/deceptive moves and throughout we reflect on the meaning of the research for sports and sport-related research, considering potential research directions and applications.

In writing this review and selecting research to include, it is important to acknowledge that action experiences integrate many components and in much of the research it is hard to disentangle motor from visual experience. Further, we can only speculate on the bidirectional influences of action on perception and perception on action. Action experiences affect what you see, but what you see will also affect what you do. In addition, these experiences will change sensitivity for context and objects as well as rule-based knowledge structures.

The action observation network and “mirror properties”

The AON is a neural umbrella network that is activated when humans visually perceive and observe other humans involved in actions. This network comprises all brain areas that are activated by the mere observation of actions (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009). Many of the studied actions have not been embedded in a sports context. Based on a meta-analysis of 104 studies with predominantly hand-actions, this network was reported to involve: the inferior frontal gyrus (IFG, BA44/45), the dorsal and ventral premotor cortex (dPMC, vPMC), the inferior parietal lobule (IPL), the superior parietal lobule (SPL), the inferior parietal sulcus (IPS), some sections of the primary somatosensory cortex (S1) as well as the primary motor cortex (M1), the posterior medial temporal gyrus (pMTG), the fusiform face/body area (FFA/FBA) and visual area V5 (Caspers, Zilles, Laird, & Eickhoff, 2010). We have included a figure highlighting these areas (see Figure 1) as well as a table detailing key brain areas mentioned throughout this review and associated abbreviations (Table 1). It should be noted, from an analytical level, that many of the areas in this network are relevant for many different processes and functions, beyond those implicated in action observation.

One body of research that underpinned the AON and subsequent research is the mirror-neuron domain. Over twenty years ago, using single-cell recordings, these neurons were uncovered in area F5 of the monkey premotor cortex (comparable to the human vPMC). These were so called as they discharge both when a particular action is executed and when a similar action is observed (e.g., di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; for a review, see Rizzolatti & Craighero, 2004). In further experiments, Rizzolatti and other groups found neurons with similar properties also in the IPL as well as the IFG (adjacent to the primary motor cortex, e.g., Buccino, Lui, et al., 2004). In the decades since, extensive research has been conducted to determine the presence and properties of an analogous 'mirror neuron system' (MNS) in humans. Despite such efforts, the likely neural substrates of these mirror regions remain controversial and there is still a conceptual and methodological controversy about 'mirroring' per se. The vast majority of investigations involving humans have been performed using non-invasive, neuroimaging and neurophysiological methods, providing only indirect evidence of the existence of the MNS (for reviews, see e.g., Cattaneo & Rizzolatti, 2009; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001). However, isolated studies of single neuron recordings in the human brain have corroborated evidence of action observation-execution matching neurons (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010).

Activation likelihood estimation (ALE) meta-analysis, performed on 125 studies, has provided a quantitative index of the consistency of patterns of fMRI activity measured in human studies of action observation and action execution (Molenberghs, Cunnington, & Mattingley, 2012). Surprisingly, the authors reported a much broader network than expected from the existing data, with 14 separate clusters identified as having “mirror properties”. New clusters included the primary visual cortex (V1), the cerebellum and parts of the limbic system. The authors argued for the existence of a brain network engaged in action observation and action execution that is complemented with areas relevant for non-motor functions (auditory, somatosensory, affective, etc.). Similar ideas regarding a widely distributed multisensory network in the brain involved in sensorimotor matching between visual and motor aspects (including the SPL and the precuneus), have also been suggested by others (Cisek & Kalaska, 2010; Filimon, Rieth, Sereno, & Cottrell, 2015; Ghazanfar & Schroeder, 2006).

Despite questions regarding the straightforward claim that the observation and execution of the same action solicit identical neural structures in the brain, logically, this could only happen when the observer is able to execute the observed action. Based on that, Rizzolatti et al. (2001) proposed that observation of actions within the viewer's motor repertoire could be mapped onto the viewer's own motor representations of the action. For humans, it was assumed that this common coding would result in observers covertly simulating the actions they perceive (Jeannerod, 2001). Actions outside of the viewer's motor repertoire should then not elicit the motor system and instead should be processed more visually (e.g., Buccino, Lui, et al., 2004; Stevens, Fonlupt, Shiffrar, & Decety, 2000). In this literature, motor system activation during action observation is thought of as a low-level simulation of the action (also referred to as 'motor resonance,' e.g., Rizzolatti & Craighero, 2004). This resonance or simulation is proposed to contribute to a number of cognitive functions, including action understanding (e.g., Rizzolatti & Craighero, 2004) and anticipation of action outcomes (for overviews, see Wilson & Knoblich, 2005; Zentgraf, Munzert, Bischoff, & Newman-Norlund, 2011; for empirical studies, see Balser et al., 2014a,b; Bischoff et al., 2012, 2014; Mulligan, Lohse, & Hodges, 2016a,b; Munzert, Zentgraf, Stark, & Vaitl, 2008).

When action and sport experiences are gathered, actors do not only build up procedural memories about how to act, they also build up episodic memories which allow processing of contingencies between bodily movements and their sensory and environmental consequences (e.g., Wolpert & Flanagan, 2001). For example, after dribbling towards the goal; a shot, a pass or a turnover are likely action consequences for goalkeepers anticipating actions of outfield players in soccer. Concomitantly, skilled actors or sports performers observe actions with experience-based expectations of the upcoming actions and they might also be able to prepare certain actions based on their observations or normative biases (e.g., Bar-Eli, Azar, Ritov, Keidar-Levin, & Schein, 2007; Leuthold, Sommer, & Ulrich, 2004). There is evidence that the brain spontaneously exploits frequency-based structure in observed action sequences (e.g., Ahlheim, Stadler, & Schubotz, 2014) and that this sensitivity shows up in MNS areas, as well as the IPS and prefrontal cortex.

Conceptually, motor contributions to observation can be widespread, going beyond activation of actions to estimation of time, physical events and mental rotation (e.g., Coull, Nazarian, & Vidal, 2008; Press & Cook, 2015; Schubotz, 2007; Wohlschläger, 2001). Researchers have shown that the AON is sensitive to unexpected actions (e.g., Schiffer, Ahlheim, Ulrichs, & Schubotz, 2013) and there is evidence that vPMC activation increases with the available number of object-related actions, presumably related to some competition process in action selection (Schubotz, Wurm, Wittmann, & von Cramon, 2014). Which specific aspect of one's own action experiences causally impacts on action observation is still under debate, but it should be acknowledged that the motor system is involved in observation of events per se, not only in dynamic human action observation.

Neurophysiological methods

The common methods used in investigations presented in this review are briefly detailed below. These include; electroencephalography (EEG), transcranial magnetic stimulation (TMS) coupled with electromyography (EMG), and functional magnetic resonance imaging (fMRI). It must be acknowledged that these are not direct measures of neuronal activity such as single cell recordings, which are typically reserved for animal studies (*cf.*, Mukamel et al., 2010).

EEG provides a means to capture summed neural activities at a very high temporal resolution (Nakata, Yoshie, Miura, & Kudo, 2010) and there are many EEG parameters available. It has been shown that the mu rhythm recorded over the motor cortex as well as alpha and beta band oscillations (captured over sensorimotor cortical areas within the frequency band of 8-13Hz) decrease in power during both the execution and observation of action (e.g., Babiloni et al., 2002; Cochin, Barthelemy, Roux, & Martineau, 1999; Muthukumaraswamy, Johnson, & McNair, 2004; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997). This activity is referred to as event-related desynchronization (ERD), and is thought to reflect activity of the MNS (e.g., Lepage & Théoret, 2006; Rizzolatti & Craighero, 2004; for a review, see Pineda, 2005). The veracity of mu rhythm suppression as a marker of MNS activity has been supported through studies where both fMRI and EEG have been collected simultaneously (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011). A meta-analytic review of 80 studies showed that mu suppression was sensitive to action observation, yielding a moderate effect size of d = .31, and execution, d = .46 (Fox et al., 2016).

The use of TMS in investigating processes during action observation follows the rationale that the perception of bodily motion (and skilled motion in particular) changes neural excitability in the primary motor cortex (M1). By applying TMS to the primary motor cortex during the viewing of actions, enhanced corticospinal activity can be captured using EMG of the motor evoked potentials (MEPs – measures of corticospinal excitability) in the effector(s) involved in the viewed action (typically hand, arm, or foot muscles) (e.g., Fadiga, Fogassi, Pavesi, &

Rizzolatti, 1995). Using this technique, it has been shown that the motor neuron response elicited by the observation of an action is sensitive to the observed task requirements (e.g., weight lifted, Behrendt, de Lussanet, Zentgraf, & Zschorlich, 2016), and temporally coupled to the actual execution of that same action (Gangitano, Mottaghy, & Pascual-Leone, 2001).

Functional MRI (fMRI) is probably the most commonly used technique to show how action observation involves the motor system and depends upon the skillset of the observer. This method of neuroimaging maps brain activity by measuring the blood-oxygen-level-dependent (BOLD) signal. While this tool obviously constrains the tasks that can be examined (movement is prevented or significantly restricted inside the scanner), it has been useful in capturing differences in response to a variety of visual stimuli as a function of the observers' individual motor repertoires. However, labeling an elevated BOLD signal in an fMRI study as signaling pure MNS activation must be regarded with caution, as it is known from direct recordings that only some neurons in this area have mirror properties. Although fMRI has its strengths in providing a valid spatial marker of changed neural processing, traditional approaches on the basis of subtraction logic and univariate analyses bear issues that constrain clear-cut conclusions. More advanced approaches (e.g., multi-voxel pattern analysis and diffusion-tensor imaging), have helped to broaden understanding.

Over the last decade, the notion of experience-dependent motor simulation has gained substantial interest from neuroscience. In what follows, we review current literature that speaks to how the recruitment of the simulation circuit during action observation is modulated by a broad range of processes related to the viewer's own action experiences. We briefly consider developmental work on this topic and studies related to short-term manipulations and then expertise-related effects of relevance to sports.

Action observation and recruitment of the simulation circuit: A review of the evidence

Early action experiences

In order to help understand the potential significance of the AON system in adults that is responsive to motor experience, it is worthwhile briefly considering its sensitivity to motor development. Neonatal, behavioural imitation research has been interpreted by some to speak to the innate presence of a MNS (for a review, see Lepage & Théoret, 2007; for relevant critical commentaries see also Bertenthal & Longo, 2007; Kilner & Blakemore, 2007). There is also some neurophysiological-based research supporting the existence of a MNS within the infant brain (e.g., Cochin, Barthelemy, Roux, & Martineau, 2001; Lepage & Théoret, 2006; Nyström, 2008), as well as its modulated recruitment during action observation as a function of action experience (Southgate, Johnson, Osborne, & Csibra, 2009) and growing motor capabilities (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008).

Mu- and beta-desynchronization in 14-16 mo infants were greatest when infants observed crawling versus walking videos, which was the motor primitive with which all infants had more experience (van Elk et al., 2008). The size of this effect was positively correlated with experience crawling. Similar results were shown in a study of 18-30 mo infants watching goal-directed and imitated (non-goal directed) actions (Warreyn et al., 2013). Mu suppression (recorded from central electrodes), was correlated with the quality of a child's imitation, pointing to its functional significance and coupling to the motor capabilities of the child. However, the relative mu suppression seen during action observation in young infants (14 mo) compared to mu suppression during action execution is less than that typically shown in adults, reflecting the sensitivity of this system to development (Marshall, Young, & Meltzoff, 2011).

Researchers have also shown how the action-observation response is sensitive to the development of anticipatory skills in young infants. A unilateral (left hemisphere – alpha band) desynchronization was seen during observation, but it was only shown once infants could anticipate the forthcoming reach (Southgate et al., 2009). This suggests that it indexed a predictive response to action observation (bilateral desynchronization was seen during actual reaching).

The extant research in infants provides evidence that even early in life, action experiences and abilities modulate the perception of action (e.g., van Elk et al., 2008) and that the changed motor processing elicited during observation may subserve action anticipation (Southgate et al., 2009). These points will be further elucidated in the following sections, as we consider the emergence and effects of motor-experience-dependent observation in adult populations.

Physical and imitative short-term practice

One of the advantages of short-term motor learning studies is the potential for control of action and visual experiences. As some of the best examples of this type of research, two dance-training studies were conducted involving both behavioural and brain activity measures. In the first study, expert dancers physically practiced dance sequences for 5 weeks and underwent fMRI scanning while watching these as well as control (novel) sequences (Cross, Hamilton, & Grafton, 2006). As the dancers accrued more physical experience, they exhibited increased activity in the AON during observation and imagery of the rehearsed compared to the untrained sequences (differentiated by greater activity within the STS, vPMC, IPS and SMA). Activation within the IPL and vPMC was positively correlated with the dancers' judgments of how well they could perform the movements (Cross et al., 2006; see also Gardner, Goulden, & Cross, 2015). These results provided evidence that the simulation circuit is tuned to the motor repertoire of the observer, even for short-term practice in experienced dancers (Cross et al., 2006).

In a follow up study of novice dancers, playing a dance-based video game for five days, significant training-related changes in the AON were shown (Cross et al., 2009). Although there were differences in activation as a function of physical or observational experiences, there was also overlap, particularly in the left-IPL and the right-PMC regions, as a result of either experience, compared to watching novel sequences. However, it was only physical experience that produced a significant correlation between behavioural measures of performance and activity in the PMC. Competency, rather than improvement across practice, was most strongly related to AON activation.

Despite increases in activation in the AON as a function of action and visual experiences, these experiences have also led to decreased activation in AON areas. For example, observation of unpracticed chords on a guitar evoked stronger activation in the AON compared to chords that had been practiced (physically imitated) (Vogt et al., 2007). The authors suggested that recruitment of the AON might be sensitive to the intention behind action observation, where intention to imitate decreases AON activation for practiced items. Across two studies there was increased activation within the fronto-parietal circuit (vPMC and IPL) during action observation and subsequent imitation of the unpracticed guitar chords compared to the practiced chords, which was proposed to reflect the breaking down of unfamiliar actions into familiar elements in order to imitate (Higuchi et al., 2012; Vogt et al., 2007). In other work, observation without intention to imitate enhanced motor resonance for practiced items (e.g., judgments about ability to perform or the aesthetics of a movement, Calvo-Marino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross et al., 2006; see also Buccino, Vogt, et al., 2004; Higuchi, Holle, Roberts, Eickhoff, & Vogt, 2012). A decrease in activation with practice might also signal greater efficiency in action preparation, or potentially a familiarity effect associated with the lack of surprise in the stimuli.

Insight into short-term, experience-dependent action observation has also been gained through the use of EEG. Brief action experience with unfamiliar drawing actions was shown to bring about changes in the neural activity of later observations, specifically with respect to mu rhythm desynchronization at central sites (Marshall, Bouquet, Shipley, & Young, 2009). The fidelity with which the imitated action was executed was positively correlated with mu band desynchronization during observation (see also Casile & Giese, 2006). The imitation condition also resulted in greater EEG desynchronization at sites overlying the dorsolateral prefrontal cortex (DLPFC) compared to a control condition (performing a familiar writing movement). When the length of the training session was increased, no differences were observed between an observation-only group and a combined physical practice and observation group (Quandt, Marshall, Bouquet, Young, & Shipley, 2011). Although both showed more desynchronization than seen for novel actions, mu suppression differences as a function of practice were only noted in frontal electrode sites.

One of the advantages of EEG in such short-term studies of action experiences is that EEG can be collected in close proximity to the actual physical (or observational) practice trial, such that changes in EEG during practice can be correlated to changes at a subsequent observation period as well as with behavioural measures. This concurrent charting will allow a better understanding of the relationship between these processes and the timescale of respective changes. Because action experiences modulate the action observation-execution matching system within mere hours, this raises concerns about the discriminant validity of such cortical markers of skill. Evidently, there is still much unknown regarding the timescale of the development of skilled observation, with the most intensive training manipulation to date comprising just 5 weeks (Cross et al., 2006). Does the neurophysiological development of this system follow a power function, analogous to the Law of Practice (e.g., Crossman, 1959; Lee & Wishart, 2005), such that it might undergo dramatic changes early in practice, with incrementally smaller changes over time? It is possible, of course, that after a certain refinement of an action, further fine-tuning ceases to significantly influence perceptual-cognitive and/or neural processes, or at least those captured by current measures. Among recreational golfers, those individuals who had the more “intense” training (i.e., required fewer days to complete 40 hours of training) showed more grey matter changes in the parieto-occipital junction and vPMC, although these individuals were also of a higher proficiency at the start of the study (Bezzola, Mérillat, Gaser, & Jäncke, 2011).

There also needs to be a better discrimination of action and visual experiences to determine their differential impact on brain neurophysiology and what this means with respect to efficiencies and effectiveness of training. Are combined experiences (visual-motor) better than either in isolation, especially when given in an alternating schedule whereby small blocks of observation are followed by small blocks of physical practice? This schedule is most reminiscent of practice in the field where demonstrations typically precede practice attempts and then are interspersed throughout later attempts (see also Ong & Hodges, 2012; Zentgraf et al., 2011). Related to this issue, studies where individuals learn without vision (e.g., Casile & Giese, 2006; Mulligan & Hodges, 2014) could elucidate how each type of experience uniquely contributes to changes in brain neurophysiology.

The fact that visual familiarity has been shown to increase cortical activity during action observation compared to the viewing of novel stimuli (e.g., Cross et al., 2009), shows that the AON is not only sensitive to physically acquired (motor) experiences. Brief physical practice and distinct observational practice have been shown to result in similar motor resonance during subsequent action observation, although only in the frontal-parietal mirror circuit and not in lower-level motor-related circuits associated with the motor-cingulate-basal-ganglia (Higuchi et al., 2012). The potential benefits of observational practice when physical training is not a viable option remain of interest (e.g., during rest intervals in athletic training, injury recovery periods, rehabilitation). There is some suggestion that observational practice during the retention interval of a physically practiced skill aids later retention and activation of mirror-related circuits (Zhang et al., 2011). There has also been evidence that combining observational practice with peripheral nerve stimulation (i.e., activation of the afferent system), leads to changes in the brain that are enhanced compared to observational practice alone (Bisio et al., 2015).

An alternative form of practice that has not yet been studied with respect to its potential influence on the AON is passive physical practice, where the body is guided through the motions in the absence of the individual’s actively generated motor commands. Though such forms of passive physical practice do not typically support learning compared to active physical practice (for a review, see Hodges & Campagnaro, 2012), whether such action experiences are sufficient to promote the strengthening and/or building of cortical connections remains to be seen, and may be of particular relevance with respect to special populations or in situations where safety is a concern. Physical guidance is still popular in the teaching of gymnastic skills, such that cortical processes engaged following such guidance training may alert to the potential efficacy of this training as well as to the types of experiences which engender change in the AON.

In summary, these studies give evidence for the involvement of the AON following short-term experiences. They show that the extent to which the AON is activated during action observation is related to the similarity between the perceived action event and the viewer's relevant motor representation. In these final sections, we review studies that have mostly involved cross-sectional comparisons of elite athletes in sports, in order to determine what neurological processes (and experiences) might be related to the expert advantage in perceptual-cognitive skills.

Sport expertise and long-term visual-motor experiences

The previous section highlighted research that provides insight into how brief action experiences modulate action observation in the early phases of motor learning. At the other end of the experience spectrum, some 10,000 hours of practice later are the (visual)-motor experts (Ericsson, Krampe, & Tesch-Romer, 1993). These immensely dedicated individuals have reached the highest levels of motor performance and acquired the most specialized motor repertoires. Athletes in highly dynamic, open sport environments have also acquired perceptual-cognitive skills that appear to underpin their success in the field (for a meta-analysis see Mann, Williams, Ward, & Janelle, 2007). As a result, these individuals have developed truly 'skilled' observation. It is this subset of the general population that has inspired and enabled the research presented below, where we specifically focus on experts in sport. We review three broad areas of research relevant to skilled observation in sport and the brain; 1) observation as a function of action familiarity, 2) observation during predictive decisions and 3) observation processes engaged during judgments about deceptive actions.

Action-observation as a function of familiarity. The research program of Calvo-Merino and colleagues (2005, 2006) provides an illustrative example of the modulating effects of motor expertise on the perception of action. These authors used fMRI to study the brain activity of expert ballet dancers (males and females) and capoeira martial artists during the observation of actions specific to each specialty or gender. Even though the dancers were asked to report on the aesthetics of the observed actions, increased neural activity was shown in the premotor and parietal brain cortices (areas implicated in the MNS) when movements were observed that were within the dancers' own specialized motor repertoires (e.g., ballet for ballerinas). Because expert male and female ballet dancers who trained together also showed greater activation in motor regions of the cortex and cerebellum when watching videos of their own gender-specific movements, the authors concluded that people simulate observed actions in terms of their own motor representations of the actions, not only in terms of shared visual experiences (Calvo-Merino et al., 2006). The fact that neural activity is differentiated within a subset of elite performers, who are only differentiated with respect to sex or type of dance, is important, as it shows the sensitivity of this network to specific action experiences.

Since these studies of dancers, various replications have been conducted across a number of different sports, including studies of archers, performers in racquet sports (tennis and badminton), as well as volleyball and soccer experts (e.g., Balser et al., 2014a,b; Bishop, Wright, Jackson, & Abernethy, 2013; Kim et al., 2011; Wright, Bishop, Jackson, & Abernethy, 2010, 2011, 2013). For example, in an fMRI study of archers, in addition to greater activation of the AON in expert archers compared to non-archers, the archers also exhibited greater recruitment of the dorsomedial prefrontal cortex (DMPFC), cingulate cortex, retrosplenial cortex, and parahippocampal gyrus compared to their untrained counterparts (Kim et al., 2011). These areas have been implicated in episodic memory retrieval and as such, the authors attributed activity in these areas to the archers' enhanced familiarity with and meaningfulness of these stimuli (i.e., top-down influences, which may be related to Ericsson and Kintsch's long-term working memory ideas provided in 1995).

Complementary to the above neuroimaging findings, event-related desynchronization (ERD) in the alpha and beta bands was responsive to the viewer's motor repertoire in a comparison of professional dancers and non-dancers viewing videos of dance and everyday movements (Orgs et al., 2008; see also Pineda, 2005). However, results contrasting to these have also been shown (rhythmic gymnastics, Babiloni et al., 2009; karate, Babiloni et al., 2010). Alpha ERD was lower in the elite compared to the less skilled groups during action observation, with the "somewhat skilled", amateur athletes, showing intermediate cortical activity (Babiloni et al., 2010). Alpha ERD was also lower in skilled observers when they provided relatively accurate judgments of the observed actions, compared to inaccurate judgments (Babiloni et al., 2009). The authors interpreted the less pronounced alpha ERD as an index of "neural efficiency," akin to that captured in skilled athletes during action execution (e.g., Baumeister, Reinecke, Liesen, & Weiss, 2008; Milton, Solodkin, Hlustik, & Small, 2007).

Despite the differences in findings, reminiscent of discrepancies in fMRI studies following short-term practice, these data support the notion that action experiences modulate the neural networks underpinning action observation. Although EEG may not be as sensitive as fMRI to experience-related changes in brain function, in addition to being a relatively inexpensive technique, EEG has the advantage of high temporal resolution compared to fMRI. The ability to capture the temporal dynamics of action observation provides opportunities to probe the predictive versus reactive nature of specific neural responses to observed action events (e.g., Southgate et al., 2009), although to date, rarely has it been used in this way in a sports-related context (*cf*. Amoruso et al., 2014; Jin et al., 2011).

Cross-sectional comparisons of amateur, intermediate, and more elite groups, alert to the sensitivity of these neural markers or probes to characterize motor experience (e.g., Babiloni et al., 2010), in addition to the somewhat more common comparisons between strictly novice and expert groups (e.g., Kim et al., 2011; Orgs et al., 2008). However, the question remains as to how sensitive the MNS or AON is to the amount of physical training (e.g., Marshall et al., 2009). Among an fMRI study of skilled basketball players, there were no behavioural (anticipation accuracy) differences as a function of visual-motor experience (and presumably no experience-based scaling of cortical activations) despite experience ranging from 468-6552 hours of practice (Abreu et al., 2012). Further research is required to assess these potential skill-based interactions and the degree of match between motor skill/experiences, perceptual-cognitive performance, and neural substrates and circuitry associated with action observation. Neural activation during perceptual-cognitive activities is likely not simply contingent upon the number, but also upon the quality of practice hours accrued (Bishop et al., 2013). Research with elite, retired athletes has the potential to inform about the permanency of these experience-related changes, especially when capabilities change.

As briefly noted, current neurophysiological measurement techniques greatly limit the movements that can be carried out by participants. While some sport researchers have attempted to require more realistic responses to visual stimuli in behaviour-based studies (e.g., Farrow & Abernethy, 2003; Mann, Abernethy, & Farrow, 2010; Mann, Abernethy, Farrow, Davis, & Spratford, 2010), neurophysiology-based investigations overwhelmingly feature unnatural perception-action responses. For example, a key-press prediction of ‘in’ or ‘out’ is clearly not a basketball player’s normal reaction to a free-throw (e.g., Abreu et al., 2012; Aglioti, Cesari, Romani, & Urgesi, 2008), and this uncoupling may misrepresent experts’ and novices’ true anticipatory skill (Farrow & Abernethy, 2003) as well as the neural processes recruited during more realistic action observation scenarios (Mann, Abernethy, & Farrow, 2010). As the intention with which action observation is undertaken has been shown to modulate the underlying neural processes (e.g., Buccino, Vogt, et al., 2004), it is also of interest whether an intent to respond differentially activates the MNS, perhaps also as a function of the instructional context (e.g., whether the response should comprise a complementary or emulative action, see Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007).

Modulation of action-observation ‘on the fly,’ so to speak, also poses interesting questions for the study and understanding of sport expertise and behavioural changes that accompany skilled observation. How might observation and perceptual-cognitive performance be affected were they executed during the course of action production? Behaviourally, there is mixed evidence regarding how the congruency of concurrently performed and observed actions impede or facilitate, for example, action-perception (e.g., Hamilton, Wolpert, & Frith, 2004; Miall et al., 2006; Müsseler & Hommel, 1997; for a review, see Schütz-Bosbach & Prinz, 2007) and action-anticipation (Mulligan et al., 2016a,b). Whether a neurophysiological basis for such effects might be discernable is obviously again challenged by the movement constraints of neuroimaging and electrophysiological measurement techniques. However, it is feasible that some small-scale actions would be possible even within a scanner environment (e.g., holding differently weighted boxes during perceptual judgment tasks, similar to Hamilton et al., 2004, or pressing against a force plate during anticipation tasks, as per Mulligan et al., 2016a,b). Moreover, alternative solutions to this limitation may not be too far off. A neurophysiological technique that has gained in popularity is tDCS (transcranial Direct Current Stimulation). Like methods involving repetitious firing of TMS (rTMS), it is possible to stimulate a specific area of the brain with effects lasting after the stimulation, such that movements are no longer constrained. tDCS works by passing a low voltage current through an area of interest, essentially changing neural excitability. It is an inexpensive method, although there is a need to know where to apply the stimulation, which might require whole brain fMRI before application. To date, tDCS has not been used to study the cortical simulation circuit, yet see Reis et al. (2009) and Banissy and Muggleton (2013) for a consideration of its potential value in motor learning and sports training, respectively.

Action anticipation. While it is clear from the literature that motorically skilled individuals are processing familiar actions differently than their unskilled counterparts, the question remains as to the functional value of brain-related differences in observation. Recent sport expertise research sheds some light on this question, as investigators have sought to determine the neural basis of elite athletes' superior perceptual-cognitive skills, with particular focus on the anticipation of action outcomes and detection of deceptive actions (see also Smith, 2016; Yarrow, Brown, & Krakauer, 2009).

The predictive brain has become a bit of a buzzword in cognitive neuroscience (Friston, 2011). When talking about action anticipation in sports, it is mostly studied as a change prediction referring to an observable event. Dynamic predictions are differentiated from probabilistic, semantic and episodic predictions (for further details, see Schubotz, 2015). Dynamic forward predictions are related to information about events unfolding in time, such as judging and/or intercepting a moving ball or anticipating the next move or action effect from a person preparing to serve or dribbling a ball

In much of the literature in the anticipation domain, the motor system's involvement in action perception is suggested to contribute to the prediction of observed action effects, potentially via forward models (e.g., Eskenazi, Grosjean, Humphreys, & Knoblich, 2009; Gorman, Abernethy, & Farrow, 2013; Wilson & Knoblich, 2005; Yarrow et al., 2009). In computational models of motor control, forward models are the sensory consequences of self-generated action that are predicted based on an (efference) copy of the motor command (Miall & Wolpert, 1996). It has been proposed that when this system is activated via action observation, there is not only a simulation of the action in terms of the viewer's own motor representation, but, as a corollary effect, a forward model is generated (although perhaps at a more general level of specificity), such that others' actions also elicit forward predictions of anticipated effects (Miall, 2003; Wolpert, Doya, & Kawato, 2003). The resultant sensory predictions are thought to be available to and influence cognitive processes, including the perception and anticipation of action events in others (e.g., Bischoff et al., 2012, 2014, 2015; Eskenazi et al., 2009; Frith, Blakemore, & Wolpert, 2000; Kilner, Friston, & Frith, 2007; Miall et al., 2006; Schubotz, 2007; Schubotz & von Cramon, 2003; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001; Zentgraf et al., 2011).

As the first functional imaging study devoted to anticipatory skill in sport, Wright and Jackson (2007) identified the neural correlates separately implicated in the viewing of sport-related motion and action, and the anticipation and judgment of action outcomes. Novice tennis players were shown videos of serves, non-serve actions (ball bouncing), and static control sequences. Using temporal occlusion (whereby videos are stopped at key points as the action and outcome unfolds), the serve sequences were edited pre- or post-ball-racquet contact and predicted directions were made by pressing a button whilst in an fMRI scanner. Compared to ball bouncing, serve sequences demanding an anticipatory judgment elicited increased activity in MNS brain areas, specifically, regions in the parietal lobule (bilateral IPL, right SPL) and in the right frontal cortex (dorsal and ventral regions of the IFG). This pattern of activation was separate from the responses in areas of the brain associated with the general viewing of motion and body actions (middle temporal visual area, STS). Considering that only novice participants were included, the results suggest that the MNS can be recruited for action prediction even when observing relatively unpracticed actions.

In a cross-sectional comparison of expert, intermediate, and novice badminton players predictions of an opposing player's shot direction, early occlusion led to increased activity in the PMC and the medial frontal cortex compared to late occlusion (Wright et al., 2010). Experts showed increased activation compared to intermediates and novices in the dPMC, ventrolateral frontal, and medial frontal cortices (areas implicated in the observation, understanding, and preparation of action), particularly when relying solely on early movement cues. In a tennis and a volleyball directional anticipation task involving comparisons of experts in these sports, in both expert groups, enhanced signals were specifically noted in the SPL, the supplementary motor area (SMA), and the cerebellum only when observing stimuli of their own sports domain (Balser et al., 2014a). We have included a figure detailing some of the results from this study, showing contrast estimates from the SPL (right), preSMA (left) and cerebellum (left) for the volleyball and tennis players in response to volleyball and tennis predictions (see Figure 2a). Below this we have also provided an illustration of brain activation differences in the preSMA area (when comparing domain expert vs. domain novice differences in anticipation) (Figure 2b). The authors suggested that the cerebellum involvement might reflect the usage of a predictive internal model (Balser et al., 2014a). In general, this research is congruent with the idea that experience performing an action prompts a low-level movement preparation which aids the expert in making anticipatory decisions (see also Balser et al., 2014b; Cacioppo et al., 2014; Wimshurst, Sowden,

& Wright, 2016 for related delineations based on tennis, volleyball, and field-hockey).

Fronto-parietal components of the AON were similarly activated during expert and novice basketball players' prediction of the fate of a basketball free throw shot (i.e., in or out, Abreu et al., 2012). Experts showed increased activation in the extrastriate body area (EBA) during the prediction task compared to a non-prediction control task, which the authors suggested was an effect of the athletes' reliance on and interpretation of body kinematics in predicting the outcomes of others' actions (see also Abernethy & Zawi, 2007; Aglioti et al., 2008; Wright et al., 2011). When watching errors, experts also showed increased activation in the bilateral IFG (specifically pars orbitalis) and right anterior insular cortex, areas associated with error monitoring and awareness (Abreu et al., 2012; see also Aglioti et al., 2008, for TMS-based evidence of elite basketball players' superior ability to predict action outcomes based on early body kinematics, and their enhanced sensitivity to errors).

Although not based on neurophysiological methods, motor-based simulation mechanisms have also been implicated in short and longer-term practice experiences in predictions of dart outcomes. In a series of studies, an action-incongruent secondary task (i.e., pushing lightly against a force gauge with the throwing arm), interfered with prediction accuracy amongst physically (not perceptually) trained individuals (Mulligan et al., 2016a,b). What's important about this work is that prediction accuracy was linked to motor-based interference. Although no measures of brain activity were taken during these anticipatory decisions, there was evidence that the areas or processes responsible for action execution needed to be "available" in order to aid action prediction accuracy. Using TMS, temporary disruptions to the motor cortex have been shown to impair recognition and anticipation of others' actions (Michael et al., 2014; Stadler et al., 2012). It appears that the action-interference effect is not only specific to action experiences, but it can erased by perceptual training (Mulligan & Hodges, 2016). This suggests that motor-related brain mechanisms that operate during action prediction are either not automatic, or that (assuming time allows), they can be overridden by more strategic, perceptually-based mechanisms (Mulligan & Hodges, 2016).

Detection of deceptive actions. It might be expected that motor resonance among skilled athletes would be sensitive to detection of errors and deceptive actions given a discrepancy between an athlete's expectations and actual outcomes. However, if an athlete is likely to activate their own motor program for action when viewing an action that has a surprising ending, it may be that they will more likely be deceived. Indeed, the research seems to highlight some potential discrepancies, depending on the methods used to study deception.

Observers ranging in soccer experience were classified as low-, intermediate-, or high-skill anticipators, based on their accuracy in predicting the direction change of an oncoming soccer player (Bishop et al., 2013). When viewing deceptive actions, high-skill anticipators were distinguished from the less-skilled groups by activation within the right anterior cingulate cortex (rACC), which the authors suggested reflected the suppression of (deceived) responses to the deceptive action and the monitoring of incorrect decisions (Bishop et al., 2013). In a related study involving different skill groups, soccer players were required to determine (from a point-light model) whether i) a move by an attacker was "normal" or "deceptive" and ii) the resulting direction of the ball (Wright et al., 2013). Both conditions resulted in activation in MNS areas, and patterns of activation in these areas were sensitive to skill, with highest activations among the most skilled, male players. Detection of deceptive actions was most strongly delineated with respect to higher-level cortical processing areas (i.e., prefrontal cortex, medial frontal cortex, anterior insula, cingulate gyrus) in comparison to ball location anticipation. The authors suggested that these differences may reflect the novelty of judging deceptive actions and the cognitive effort this entails, in comparison to anticipating outcomes, which are more of an automatic consequence of observation.

TMS has also been used to show how interactions between the perceptual and motor systems affect expert athletes’ sensitivity to deceptive movements. Expert soccer kickers were more likely to be fooled by fake actions (where an observed kicker’s body kinematics and the ball trajectory did not match) than novices and expert goalkeepers (Tomeo, Cesari, Aglioti, & Urgesi, 2013). Based on MEPs in response to TMS, “fooling” actions elicited similar lower-limb motor facilitation as that seen for real actions, only in the expert kickers. Differences between goalkeepers and expert kickers suggest that anticipatory decisions are a result of different mechanisms in players who have primarily motor experience, in comparison to goalkeepers who have acquired more visual experience predicting kick direction. There have, however, been criticisms of these methods and conclusions (Mann, Dicks, Cañal-Bruland, & van der Kamp, 2013). Some of this criticism is based on the stimuli used to show “deceptive” actions (where there is no intentional modification of body kinematics by the actor, which would be better representative of “fooling”). The ability to not be fooled or identify deception is likely to be a skill that is both a product and a curse of motor expertise. Although with playing experience players should be better able to detect valid from invalid cues (as confirmed across many studies, e.g., Dicks, Uehara, & Lima, 2011; Jackson, Warren, & Abernethy, 2006; Mori & Shimada, 2013), the potential to misinterpret cues due to action simulation processes, particularly when the actions change in an unexpected way is not surprising. What remains to be established is how training might moderate these effects and potentially lead to different types of prediction processes. Although the data are only behavioural, there is evidence that motor simulation processes that are engaged to aid anticipation can be trumped by acquisition of perceptually-based strategies (Mulligan & Hodges, 2016).

In summary, the studies cited in these last three sections highlight the role of the (cortical) motor system in detecting deceptive actions and generating predictions about what might happen (and ultimately what to do) in sport-specific scenarios. There are of course limits to some of these approaches with respect to the types of tasks that can be studied and the general difficulty in assessing performance when people are realistically responding. Moreover, just because a particular area of the brain is activated during these perceptual-cognitive tasks, this still does not allow us to distinguish what participants are actually doing when they make decisions, that is, whether they access perceptual or motor images, whether they generate actions and then suppress them, whether they rely on some generative action processes in addition to recognition of past events. These techniques and ideas should, however, prompt reflection as to what it means to argue for motor-driven skilled observation and guide future inquiries into how observation and associated perceptual-cognitive activities are bound within the action capabilities of the observer.

While researchers have attended to the action experiences and performance of their observer groups, it is important for such design vigilance to extend to the actors featured in experimental stimuli. There is behavioural evidence showing that the closer the match between an actor and observer’s motor skills, the better the viewer’s action-recognition (Loula, Prasad, Harber, & Shiffrar, 2005) and action-prediction (Knoblich & Flach, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002; Mulligan et al., 2016a). Therefore, consideration of how the similarity between the actor and observer groups’ motor capabilities factors into the observers’ processing of action events, perceptual-cognitive performance and the resulting inferences is needed. To date, there have been no attempts to compare perception and anticipation differences or motor resonance when a novice performer has provided the visual stimuli in addition to the typical skilled model (although Ikegami & Ganesh, 2014, have shown that motor experts can change their predictions as a result of observing and receiving feedback about prediction accuracy when watching low-skilled models).

There has been little attempt to examine behavioural differences in perception or anticipation of self-generated (versus other-generated) sporting actions (*cf.*, Bischoff et al., 2012; Jackson, van der Kamp, & Abernethy, 2008; Knoblich & Flach, 2001; Mulligan et al., 2016a) and no attempts to study neurophysiological differences underpinning the perception of these actions. This may have implications for effective training methods (based on self vs. other observation; for a related review, see Hodges & Ste-Marie, 2013). The inclusion of self- and novice-action stimuli can provide insight into the sensitivity of action simulation systems for the anticipation of action outcomes and potentially alert as to how expert athletes' perception may be worse when action consequences are less predictable (e.g., when associated with novices' less consistent motor performance), in comparison to that of more novice or intermediate athletes. Moreover, it may be the case that novices exhibit 'skilled' levels of observation and perceptual-cognitive abilities when given the opportunity to view motor performances that more closely match their own action representations. This similarity-driven process would also raise some issues about coaching and refereeing and what type of person (in terms of past or current motor skills or experiences) would make the best perceptual-cognitive decisions (for an illustration of such interactions based on motor experience among referees, see Dosseville, Laborde, & Raab, 2011; Pizzera, 2012).

Summary and conclusions

With the advancement and wider availability of neurophysiological measurement techniques, there has been a growing interest in and understanding of the neural processes subserving action observation in recent years. This has been particularly evidenced by research into sport expertise and the human brain. There is now a compelling body of research demonstrating both the involvement of the viewer's motor system during action observation, as well as the importance of the viewer's individual motor repertoire towards a multi-faceted understanding of observed action events. Converging evidence that action experiences modulate the neural structures and circuitry recruited when watching motor performances and promote 'skilled' observation of familiar movements, has been provided through the study of motor experts and their novice counterparts, training manipulations, and natural motor development.

Even though substantial progress has been made over the last decade towards elucidating the complexities associated with experience-dependent motor resonance, there is still much to learn. The susceptibility of the AON to different forms and durations of training remains to be determined, as does the importance of the similarity between an actor and observer towards observation-induced simulation. What is important from a sports and the brain perspective is to know the sensitivity of these networks to current and future performance and whether neural signatures during action observation give insight into subsequent trainability or performance on the field. Also, it would be important to better determine how sensitive observation-induced activations in the brain are to specific skills of the performer, including such things as physical and tactical ability, creativity in decision processes, and behaviours typically demonstrated (or observed) by players in the field. The issue of transfer across domains also has the potential to be enhanced by the study of brain activations during observation to elucidate shared processes that may be involved in tactical processes (such as decision making in soccer and hockey), motor performance (e.g., jumping in hurdles vs. jumping in long jump) as well as observation for aesthetic judgments (like those required in gymnastics or ice-dancing judges) as a function of different experiences as a performer or coach.

References

Abernethy, B., & Zawi, K. (2007). Pickup of essential kinematics underpins expert perception of movement patterns. *Journal of Motor Behavior, 39*(5), 353-367.

Abreu, A. M., Macaluso, E., Azevedo, R. T., Cesari, P., Urgesi, C., & Aglioti, S. M. (2012). Action anticipation beyond the action observation network: A functional magnetic resonance imaging study in expert basketball players. *European Journal of Neuroscience, 35*(10), 1646-1654.

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience, 11*, 1109-1116.

Ahlheim, C., Stadler, W., & Schubotz, R. I. (2014). Dissociating dynamic probability and predictability in observed actions – an fMRI study. *Frontiers in Human Neuroscience, 8*, 1-13.

Amoruso, L., Sedeño, L., Huepe, D., Tomio, A., Kamienkowski, J., Hurtado, E., Cardona, J. F., Álvarez González, M. Á., Rieznik, A., Sigman, M., Manes, F., & Ibáñez, A. (2014). Time to tango: Expertise and contextual anticipation during action observation. *NeuroImage, 98*, 366-385.

Arnstein, D., Cui, F., Keysers, C., Maurits, N. M., & Gazzola, V. (2011). μ-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *Journal of Neuroscience, 31*(40), 14243-14249.

Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Cocozza, G., Del Percio, C., Moretti, D.V., & Rossini, P. M. (2002). Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: A high-resolution EEG study. *NeuroImage, 17,* 559-572.

Babiloni, C., Del Percio, C., Rossini, P. M., Marzano, N., Iacoboni, M., Infarinato, F., Lizio, R., Piazza, M., Pirritano, M., Berlutti, G., Cibelli, G., & Eusebi, F. (2009). Judgment of actions in experts: A high-resolution EEG study in elite athletes. *NeuroImage, 45*(2), 512-521.

Babiloni, C., Marzano, N., Infarinato, F., Iacoboni, M., Rizza, G., Aschieri, P., Cibelli, G., Soricelli, A., Eusebi, F., & Del Percio, C. (2010). "Neural efficiency" of experts' brain during judgment of actions: A high-resolution EEG study in elite and amateur karate athletes. *Behavioural Brain Research, 207*(2), 466-475.

Balser, N., Lorey, B., Pilgramm, S., Naumann, T., Kindermann, S., Stark, R., Zentgraf, K., Williams, A. M., & Munzert, J. (2014a). The influence of expertise on brain activation of the action observation network during anticipation of tennis and volleyball serves. *Frontiers in Human Neuroscience, 8,* 1-13.

Balser, N., Lorey, B., Pilgramm, S., Stark, R., Bischoff, M., Zentgraf, K., Williams, A. M., & Munzert, J. (2014b). Prediction of human actions: Expertise and task-related effects on neural activation of the action observation network. *Human Brain Mapping, 35*(8), 4016-4034.

Banissy, M. J., & Muggleton, N. G. (2013). Transcranial direct current stimulation in sports training: Potential approaches. *Frontiers in Human Neuroscience, 7,* 1-3.

Bar-Eli, M., Azar, O. H., Ritov, I., Keidar-Levin, Y., & Schein, G. (2007). Action bias among elite soccer goalkeepers: The case of penalty kicks. *Journal of Economic Psychology, 28*(5), 606-621.

Baumeister, J., Reinecke, K., Liesen, H., & Weiss, M. (2008). Cortical activity of skilled performance in a complex sports related motor task. *European Journal of Applied Physiology, 104*(4), 625-631.

Behrendt, F., de Lussanet, M. H. E., Zentgraf, K., & Zschorlich, V. R. (2016). Motor-evoked potentials in the lower back are modulated by visual perception of lifted weight. *PLoS ONE, 11*(6), 1-13.

Bertenthal, B. I., & Longo, M. R. (2007). Is there evidence of a mirror system from birth? *Developmental Science, 10*(5), 526-529.

Bezzola, L., Mérillat, S., Gaser, C., & Jäncke, L. (2011). Training-induced neural plasticity in golf novices. *Journal of Neuroscience, 31*(35), 12444-12448.

Bischoff, M., Zentgraf, K., Lorey, B., Pilgramm, S., Balser, N., Baumgartner, E., Hohmann, T., Stark, R., Vaitl, D., & Munzert, J. (2012). Motor familiarity: Brain activation when watching kinematic displays of one’s own movements. *Neuropsychologia, 50*(8), 2085-2092.

Bischoff, M., Zentgraf, K., Pilgramm, S., Krueger, B., Balser, N. et al. (2015). Anticipating action effects with different attention foci is reflected in brain activation. *Perceptual and Motor Skills, 120*(1), 39-56.

Bischoff, M., Zentgraf, K., Pilgramm, S., Stark, R., Lorey, B., & Munzert, J. (2014). Anticipating action effects recruits audiovisual movement representations in the ventral premotor cortex. *Brain and Cognition, 92*, 39-47.

Bishop, D. T., Wright, M. J., Jackson, R. C., & Abernethy, B. (2013). Neural bases for anticipation skill in soccer: An fMRI study. *Journal of Sport & Exercise Psychology, 35*(1), 98-109.

Bisio, A., Avanzino, L., Gueugneau, N., Pozzo, T., Ruggeri, P., & Bove, M. (2015). Observing and perceiving: A combined approach to induce plasticity in human motor cortex. *Clinical Neurophysiology, 126*(6), 1212-1220.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C. A., & Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by non-conspecifics: An fMRI study. *Journal of Cognitive Neuroscience, 16*(1), 114-126.

Buccino, G., Vogt, S., Ritzi, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron, 42*(2), 323-334.

Cacioppo, S., Fontang, F., Patel, N., Decety, J., Monteleone, G., & Cacioppo, J. T. (2014). Intention understanding over T: A neuroimaging study on shared representations and tennis return predictions. *Frontiers in Human Neuroscience*, *8*, 1-18.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex, 15*(8), 1243-1249.

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*(19), 1905-1910.

Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology, 16*(1), 69-74.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage, 50,* 1148-1167.

Cattaneo, L. & Rizzolatti, G. (2009). The mirror neuron system. *Archives of Neurology, 66*(5), 557-560.

Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience, 33,* 269-298.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience, 11*(5), 1839-1842.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (2001). Electroencephalographic activity during perception of motion in childhood. *European Journal of Neuroscience, 13*(9), 1791-1796.

Coull, J. T., Nazarian, B., & Vidal, F. (2008). Timing, storage, and comparison of stimulus duration engage discrete anatomical components of a perceptual timing network. *Journal of Cognitive Neuroscience, 20*(12), 2185-2197.

Cross, E. S., Hamilton, A. F., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage, 31*(3), 1257-1267.

Cross, E. S., Kraemer, D. J., Hamilton, A. F., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex, 19*(2), 315-326.

Crossman, E. R. F. W. (1959). A theory of the acquisition of speed-skill. *Ergonomics, 2*(2), 153-166.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research, 91*(1), 176-180.

Dicks, M., Uehara, L., & Lima, C. (2011). Deception, individual differences and penalty kicks: Implications for goalkeeping in association football. *International Journal of Sports Science and Coaching, 6*(4), 515-521.

Dosseville, F., Laborde, S., & Raab, M. (2011). Contextual and personal motor experience effects in judo referees' decisions. *Sport Psychologist, 25*(1), 67-81.

Ericsson, K. A., & Kintsch, W. (1995). Long-term working memory. *Psychological Review, 102*(2), 211-245.

Ericsson, K. A., Krampe, R. T., & Tesch-Romer, C. (1993). The role of deliberate practice in the acquisition of expert performance. *Psychological Review, 100*(3), 363-406.

Eskenazi, T., Grosjean, M., Humphreys, G. W., & Knoblich, G. (2009). The role of motor simulation in action perception: A neuropsychological case study. *Psychological Research, 73*(4), 477-485.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology, 73*(6), 2608-2611.

Farrow, D., & Abernethy, B. (2003). Do expertise and the degree of perception-action coupling affect natural anticipatory performance? *Perception, 32*(9), 1127-1139.

Filimon, F., Rieth, C. A., Sereno, M. I., & Cottrell, G. W. (2015). Observed, executed, and imagined action representations can be decoded from ventral and dorsal areas. *Cerebral Cortex, 25*(9), 3144-3158.

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., Ferrari, P. F., & van IJzendoorn, M. H. (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychological Bulletin*, *142*(3), 291-313.

Friston, K. (2011). What is optimal about motor control? *Neuron, 72,* 488-498.

Frith, C. D., Blakemore, S. J., & Wolpert, D. M. (2000). Abnormalities in the awareness and control of action. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *355*(1404), 1771-1788.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119,* 593-609.

Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2001). Phase specific modulation of cortical motor output during movement observation. *Neuroreport, 12*(7), 1489-1492.

Gardner, T., Goulden, N., & Cross, E. S. (2015). Dynamic modulation of the action observation network by movement familiarity. *Journal of Neuroscience, 35*(4), 1561-1572.

Ghazanfar, A. A., & Schroeder, C. E. (2006). Is neocortex essentially multisensory? *Trends in Cognitive Sciences, 10*(6), 278-285.

Gorman, A. D., Abernethy, B., & Farrow, D. (2013). Is the relationship between pattern recall and decision-making influenced by anticipatory recall? *The Quarterly Journal of Experimental Psychology, 66*(11), 2219-2236.

Hamilton, A., Wolpert, D., & Frith, U. (2004). Your own action influences how you perceive another person’s action. *Current Biology*, *14*(6), 493-498.

Higuchi, S., Holle, H., Roberts, N., Eickhoff, S. B., & Vogt, S. (2012). Imitation and observational learning of hand actions: Prefrontal involvement and connectivity. *NeuroImage, 59*(2), 1668-1683.

Hodges, N. J., & Campagnaro, P. (2012). Physical guidance research: Assisting principles and supporting evidence. In N. J. Hodges & A. M. Williams (Eds.), *Skill acquisition in sport: Research, theory and practice* (2nd ed.) (pp. 150-169). New York, NY: Routledge.

Hodges, N. J., & Ste-Marie, D. (2013). Observation as an instructional method. In D. Farrow, J. Baker, & C. MacMahon (Eds.), *Developing sport expertise: Researchers and coaches put theory into practice* (2nd ed.) (pp. 115-128). New York, NY: Routledge.

Ikegami, T. & Ganesh, G. (2014). Watching novice action degrades expert motor performance: Causation between action production and outcome prediction of observed actions by humans. *Scientific Reports*, *4*, 1-7.

Jackson, R. C., van der Kamp, J., & Abernethy, B. (2008). Experts do, experts see? Common coding versus perceptual experience in anticipation skill. *Journal of Sport and Exercise Psychology, 30*(S1), S95.

Jackson, R. C., Warren, S., & Abernethy, B. (2006). Anticipation skill and susceptibility to deceptive movement. *Acta Psychologica, 123*(3), 355-371.

Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage, 14*(1), S103-S109.

Jin, H., Xu, G., Zhang, J. X., Gao, H., Ye, Z., Wang, P., Lin, H., Mo, L., & Lin, C. D. (2011). Event-related potential effects of superior action anticipation in professional badminton players. *Neuroscience Letters, 492*(3), 139-144.

Kilner, J. M., & Blakemore, S. J. (2007). How does the mirror neuron system change during development? *Developmental Science, 10*(5), 524-526.

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing, 8*(3), 159-166.

Kim, Y.-T., Seo, J.-H., Song, H.-J., Yoo, D.-S., Lee, H. J., Lee, J., Lee, G., Kwon, E., Kim, J. G., & Chang, Y. (2011). Neural correlates related to action observation in expert archers. *Behavioural Brain Research, 223*(2), 342-347.

Knoblich, G., & Flach, R. (2001). Predicting the effects of actions: Interactions of perception and action. *Psychological Science, 12*(6), 467-472.

Knoblich, G., Seigerschmidt, E., Flach, R., & Prinz, W. (2002). Authorship effects in the prediction of handwriting strokes. *Quarterly Journal of Experimental Psychology, 55A,* 1027-1046.

Lee, T. D., & Wishart, L. R. (2005). Motor learning conundrums (and possible solutions). *Quest, 57*(1), 67-78.

Lepage, J.-F., & Théoret, H. (2006). EEG evidence for the presence of an action observation-execution matching system in children. *European Journal of Neuroscience, 23*(9), 2505-2510.

Lepage, J.-F., & Théoret, H. (2007). The mirror neuron system: Grasping others' actions from birth? *Developmental Science, 10*(5), 513-523.

Leuthold, H., Sommer, W., & Ulrich, R. (2004). Preparing for action: Inferences from CNV and LRP. *Journal of Psychophysiology, 18*(2-3), 77-88.

Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of Experimental Psychology: Human Perception and Performance, 31*(1), 210-220.

Mann, D. L., Abernethy, B., & Farrow, D. (2010). Action specificity increases anticipatory performance and the expert advantage in natural interceptive tasks. *Acta Psychologica, 135*(1), 17-23.

Mann, D. L., Abernethy, B., Farrow, D., Davis, M., & Spratford, W. (2010). An event-related visual occlusion method for examining anticipatory skill in natural interceptive tasks. *Behavior Research Methods, 42*(2), 556-562.

Mann, D., Dicks, M., Cañal-Bruland, R., & van der Kamp, J. (2013). Neurophysiological studies may provide a misleading picture of how perceptual-motor interactions are coordinated. *I-Perception, 4*(1), 78-80.

Mann, D. T., Williams, A. M., Ward, P., & Janelle, C. M. (2007). Perceptual-cognitive expertise in sport: A meta-analysis. *Journal of Sport & Exercise Psychology, 29*(4), 457-478.

Marshall, P. J., Bouquet, C. A., Shipley, T. F., & Young, T. (2009). Effects of brief imitative experience on EEG desynchronization during action observation. *Neuropsychologia, 47*(1), 2100-2106.

Marshall, P. J., Young, T., & Meltzoff, A. N. (2011). Neural correlates of action observation and execution in 14-month-old infants: An event-related EEG desynchronization study. *Developmental Science, 14*(3), 474-480.

Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport, 14*(17), 2135-2137.

Miall, R. C., Stanley, J., Todhunter, S., Levick, C., Lindo, S., & Miall, J. D. (2006). Performing hand actions assists the visual discrimination of similar hand postures. *Neuropsychologia, 44*(6), 966-976.

Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control. *Neural Networks, 9*(8), 1265-1279.

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., & Frith, C. D. (2014). Continuous theta-burst stimulation demonstrates a causal role of premotor homunculus in action understanding. *Psychological Science, 25*(4), 963-972.

Milton, J., Solodkin, A., Hlustik, P., & Small, S. L. (2007). The mind of expert motor performance is cool and focused. *NeuroImage, 35*(2), 804-813.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience & Biobehavioral Reviews, 36*(1), 341-349.

Mori, S., & Shimada, T. (2013). Expert anticipation from deceptive action. *Attention, Perception, & Psychophysics, 75*(4), 751-770.

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology, 20*(8), 750-756.

Mulligan, D., & Hodges, N. J. (2014). Throwing in the dark: Improved prediction of action outcomes following motor training without vision of the action. *Psychological Research, 78*(5), 692-704.

Mulligan, D., & Hodges, N. J. (2016). Evidence against the automaticity of motor simulation in action prediction: Separately acquired visual-motor and visual representations can be used flexibly to aid in prediction accuracy. *Journal of Exercise, Movement, and Sport, 48*(1).

Mulligan, D., Lohse, K. R., & Hodges, N. J. (2016a). An action-incongruent secondary task modulates prediction accuracy in experienced performers: Evidence for motor simulation. *Psychological Research, 80*(4), 496-509.

Mulligan, D., Lohse, K. R., & Hodges, N. J. (2016b). Evidence for dual mechanisms of action prediction dependent on acquired visual-motor experiences. *Journal of Experimental Psychology: Human Perception and Performance, 42*(10), 1615-1626.

Munzert, J., Zentgraf, K., Stark, R., & Vaitl, D. (2008). Neural activation in cognitive motor processes: Comparing motor imagery and observation of gymnastic movements. *Experimental Brain Research, 188*(3), 437-444.

Müsseler, J., & Hommel, B. (1997). Blindness to response-compatible stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 23*(3), 861-872.

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research, 19*(2), 195-201.

Nakata, H., Yoshie, M., Miura, A., & Kudo, K. (2010). Characteristics of the athletes' brain: Evidence from neurophysiology and neuroimaging. *Brain Research Reviews, 62*(2), 197-211.

Newman-Norlund, R. D., van Schie, H. T., van Zuijlen, A. M. J., & Bekkering, H. (2007). The mirror neuron system is more active during complementary compared with imitative action. *Nature Neuroscience, 10*(7), 817-818.

Nyström, P. (2008). The infant mirror neuron system studied with high density EEG. *Social Neuroscience, 3*(3-4), 334-347.

Ong, N. T., & Hodges, N. J. (2012). Mixing it up a little: How to schedule observational practice. In N. J. Hodges & A. M. Williams (Eds.), *Skill acquisition in sport: Research, theory and practice* (2nd ed.) (pp. 22-39). New York, NY: Routledge.

Orgs, G., Dombrowski, J.-H., Heil, M., & Jansen-Osmann, P. (2008). Expertise in dance modulates alpha/beta event-related desynchronization during action observation. *European Journal of Neuroscience, 27*(12), 3380-3384.

Pfurtscheller, G., Neuper, C., Andrew, C., & Edlinger, G. (1997). Foot and hand area mu rhythms. *International Journal of Psychophysiology, 26*(1-3), 121-135.

Pilgramm, S., Lorey, B., Stark, R., Munzert, J., Vaitl, D., & Zentgraf, K. (2010). Differential activation of the lateral premotor cortex during action observation. *BMC Neuroscience, 11*(89), 1-7.

Pineda, J. A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing." *Brain Research Reviews, 50*(1), 57-68.

Pizzera, A. (2012). Gymnastic judges benefit from their own motor experience as gymnasts. *Research Quarterly for Exercise and Sport, 83*(4), 603-607.

Press, C., & Cook, R. (2015). Beyond simulation: Domain-general motor contributions to perception. *Trends in Cognitive Sciences, 19*(4), 176-178.

Quandt, L. C., Marshall, P. J., Bouquet, C. A., Young, T., & Shipley, T. F. (2011). Experience with novel actions modulates frontal alpha EEG desynchronization. *Neuroscience Letters, 499*(1), 37-41.

Reis, J., Schambra, H. M., Cohen, L. G., Buch, E. R., Fritsch, B., Zarahn, E., Celnik, P. A., & Krakauer, J. W. (2009). Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proceedings of the National Academy of Sciences of the United States of America, 106*(5), 1590-1595.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Reviews in Neuroscience, 27*, 169-192.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience, 2*(9), 661-670.

Schiffer, A.-M., Ahlheim, C., Ulrichs, K., & Schubotz, R. I. (2013). Neural changes when actions change: Adaptation of strong and weak expectations. *Human Brain Mapping, 34,* 1713-1727.

Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new framework. *Trends in Cognitive Sciences, 11*(5), 211-218.

Schubotz, R. I. (2015). Prediction and expectation. *Brain Mapping: An Encyclopedic Reference, 3,* 295-302.

Schubotz, R. I., & von Cramon, D. Y. (2003). Functional–anatomical concepts of human premotor cortex: Evidence from fMRI and PET studies. *NeuroImage, 20*(S1), S120-S131.

Schubotz, R. I., Wurm, M. F., Wittmann, M., & von Cramon, D. Y. (2014). Objects tell us what action we can expect: Dissociating brain areas for retrieval and exploitation of action knowledge during action observation in fMRI. *Frontiers in Psychology, 5,* 1-15.

Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Sciences, 11*(8), 349-355.

Smith, D. M. (2016). Neurophysiology of action anticipation in athletes: A systematic review. *Neuroscience & Biobehavioral Reviews*, *60*, 115-120.

Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters, 5*(6), 769-772.

Stadler, W., Ott, D. V. M., Springer, A., Schubotz, R. I., Schütz-Bosbach, S., & Prinz, W. (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. *Frontiers in Human Neuroscience, 6,* 1-11.

Stevens, J. A., Fonlupt, P., Shiffrar, M., & Decety, J. (2000). New aspects of motion perception: Selective neural encoding of apparent human movements. *Neuroreport, 11*(1), 109-115.

Tomeo, E., Cesari, P., Aglioti, S. M., & Urgesi, C. (2013). Fooling the kickers but not the goalkeepers: Behavioral and neurophysiological correlates of fake action detection in soccer. *Cerebral Cortex, 23*(11), 2765-2778.

van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage, 43*(4), 808-814.

Vogt, S., Buccino, G., Wohlschläger, A. M., Canessa, N., Shah, N. J., Zilles, K., Eickhoff, S. B.,, Freund, H. J., Rizzolatti, G., & Fink, G. R. (2007). Prefrontal involvement in imitation learning of hand actions: Effects of practice and expertise. *NeuroImage, 37*(4), 1371-1383.

Warreyn, P., Ruysschaert, L., Wiersema, J. R., Handl, A., Pattyn, G., & Roeyers, H. (2013). Infants' mu suppression during the observation of real and mimicked goal-directed actions. *Developmental Science, 16*(2), 173-185.

Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin, 131*(3), 460-473.

Wimshurst, Z. L., Sowden, P. T., & Wright, M. (2016). Expert-novice differences in brain function of field hockey players. *Neuroscience, 315*, 31-44.

Wohlschläger, A. (2001). Mental object rotation and the planning of hand movements. *Perception & Psychophysics, 63*(4), 709-718.

Wolpert D. M., Doya K., & Kawato M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 358*(1431), 593-602.

Wolpert D. M., & Flanagan J. R. (2001). Motor prediction. *Current Biology*, *11*(18), R729–R732.

Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2010). Functional MRI reveals expert-novice differences during sport-related anticipation. *Neuroreport, 21*(2), 94-98.

Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2011). Cortical fMRI activation to opponents' body kinematics in sport-related anticipation: Expert-novice differences with normal and point-light video. *Neuroscience Letters, 500*(3), 216-221.

Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2013). Brain regions concerned with the identification of deceptive soccer moves by higher-skilled and lower-skilled players. *Frontiers in Human Neuroscience, 7,* 1-15.

Wright, M. J., & Jackson, R. C. (2007). Brain regions concerned with perceptual skills in tennis: An fMRI study. *International Journal of Psychophysiology, 63*(2), 214-220.

Yarrow, K., Brown, P., & Krakauer, J. W. (2009). Inside the brain of an elite athlete: The neural processes that support high achievement in sports. *Nature Reviews Neuroscience, 10,* 585-596.

Zentgraf, K., Munzert, J., Bischoff, M., & Newman-Norlund, R. D. (2011). Simulation during observation of human actions: Theories, empirical studies, applications. *Vision Research, 51*(8), 827-835.

Zhang, X., de Beukelaar, T. T., Possel, J., Olaerts, M., Swinnen, S. P., Woolley, D. G., & Wenderoth, N. (2011). Movement observation improves early consolidation of motor memory. *Journal of Neuroscience, 31*(32), 11515-11520.

Table 1: Primary areas (cited in this review) implicated in the action observation network (AON) and related to action prediction and identification of familiar or deceptive actions

General area	Specific area	Acronym	Primary study/Review article
Frontal/central	Inferior frontal gyrus	IFG	Caspers et al. (2010) Wright & Jackson (2007)
	Bilateral inferior frontal gyrus (pars orbitalis)		Abreu et al. (2012)
	Dorsal and ventral premotor cortex	dPMC/vPMC	Caspers et al. (2010) Cross et al. (2006) Cross et al. (2009) Wright et al. (2010)
	Primary motor cortex	M1	Cisek & Kalaska (2010)
	Dorsolateral prefrontal cortex	DLPFC	Cisek & Kalaska (2010) Marshall et al. (2009) Wright et al. (2010)
	Dorsomedial prefrontal cortex	DMPFC	Kim et al. (2011) Wright et al. (2010) Wright et al. (2013)
	Ventrolateral frontal cortex		Wright et al. (2010)
	Supplementary motor area	SMA	Balser et al. (2014a) Cross et al. (2006)

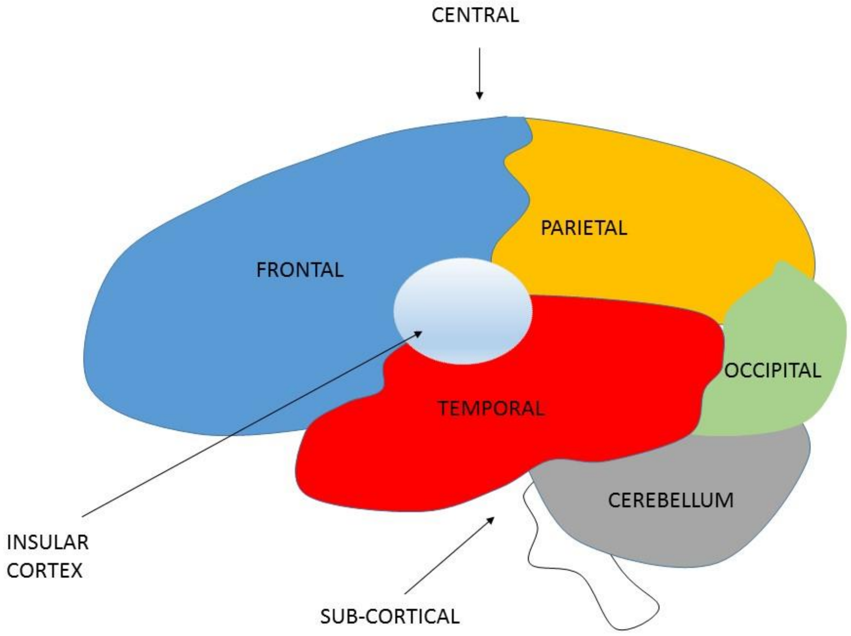
Parietal	Inferior parietal cortex/lobe	IPL	Caspers et al. (2010) Cross et al. (2009) Wright & Jackson (2007)
	Superior parietal cortex/lobe	SPL	Balser et al. (2014a) Caspers et al. (2010) Wright & Jackson (2007) Wright et al. (2013)
	Inferior parietal sulcus	IPS	Caspers et al. (2010) Cross et al. (2006)
	Primary somatosensory cortex	S1	Caspers et al. (2010)
	Precuneus		Cisek & Kalaska (2010)
Temporal	Posterior medial temporal gyrus	pMTG	Caspers et al. (2010)
	Superior temporal gyrus	STG	Bishop et al. (2013)
	Fusiform face/body area	FFA/FBA	Caspers et al. (2010)
	Fusiform gyrus		Pilgramm et al. (2010)
	Parahippocampal gyrus		Kim et al. (2011)
	Superior temporal sulcus	STS	Cross et al. (2006) Wright & Jackson (2007)
Occipital	Visual area V5	V5	Caspers et al. (2010)
	Primary visual cortex	V1	Molenberghs et al. (2012)
	Middle temporal visual area		Wright & Jackson (2007)
	Extrastriate body area	EBA	Abreu et al. (2012)

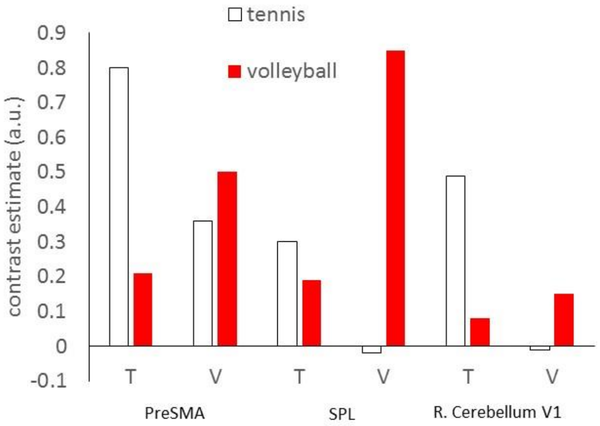
	Middle occipital cortex		Pilgramm et al. (2010)
	Occipital gyrus		Pilgramm et al. (2010)
Subcortical	Right anterior insular cortex		Abreu et al. (2012)
			Wright et al. (2013)
	Limbic system		Molenberghs et al. (2012)
	(Anterior) cingulate cortex	ACC	Bishop et al. (2013)
			Kim et al. (2011)
			Wright et al. (2013)
	Retrosplenial cortex		Kim et al. (2011)
Cerebellum			Balser et al. (2014a)
			Calvo-Merino et al. (2006)
			Molenberghs et al. (2012)

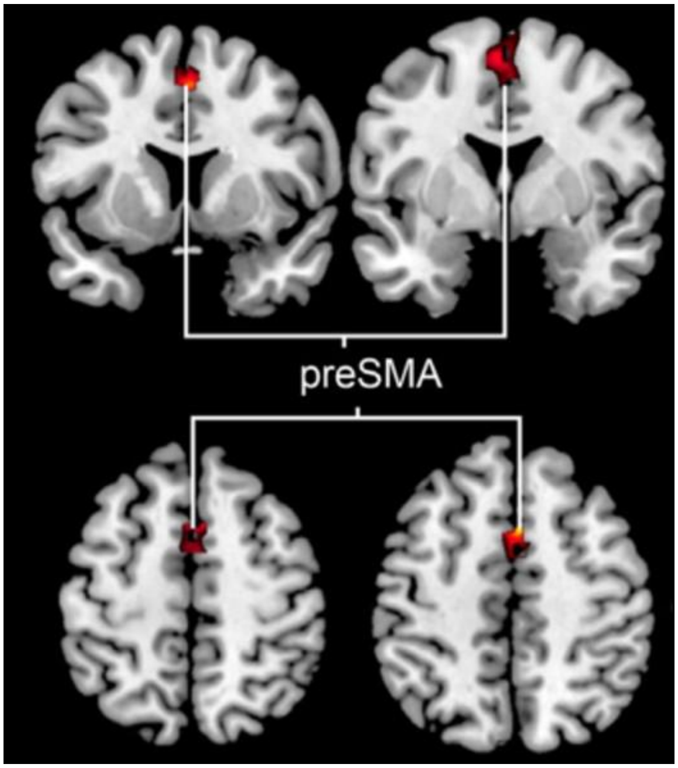
Figure captions

Figure 1: Schematized brain diagram of the cerebrum and its major brain areas and the cerebellum. Please note that the insular cortex and the limbic system lie beneath the cerebrum (i.e., subcortical).

Figure 2: a) Contrast estimates (from fMRI) in the SPL (right), preSMA (left) and cerebellum (left) for the volleyball and tennis players in Balser et al. (2014a), showing response to predictions based on volleyball and tennis stimuli (prediction activation was calculated based on a comparison to an observe-only conditions). In b) an illustration of brain activation differences in the preSMA area (when comparing domain expert vs. domain novice differences in anticipation) is shown based on a top-down view. This Figure has been adapted from Balser, N., Lorey, B., Pilgramm, S., Naumann, T., Kindermann, S., Stark, R., Zentgraf, K., Williams, A.M. & Munzert, J. (2014). The influence of expertise on brain activation of the action observation network during anticipation of tennis and volleyball serves. Frontiers in Human Neuroscience, 8 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4117995/).


CENTRAL
FRONTAL
PARIETAL
OCCIPITAL
TEMPORAL
CEREBELLUM
INSULAR
CORTEX
SUB-CORTICAL


☐ tennis
🟥 volleyball
contrast estimate (a.u.)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
T
V
T
V
T
V
PreSMA
SPL
R. Cerebellum V1


preSMA