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The role of cortical sensorimotor oscillations in action anticipation

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ABSTRACT

The human mirror neuron system is believed to play an important role in facilitating the ability of athletes to anticipate the actions of an opponent. This system is often assessed with EEG by measuring event-related changes in mu (8–13 Hz) sensorimotor oscillations. However, traditional channel-based analyses of this measure are flawed in that due to volume conduction effects mu and non-mu alpha activity can become mixed. This flaw means it is unclear the extent to which mu activity indexes the mirror system, as opposed to other processes such as attentional demand. As a solution to this problem, we use independent component analysis to separate out the underlying brain processes during a tennis-related action observation and anticipation task. We investigated expertise-related differences in independent component activity. Experienced tennis players (N=18) were significantly more accurate than unexperienced novices (N=21) on the anticipation task. EEG results found significant group differences in both the mu and beta (15–25 Hz) frequency bands in sensorimotor components, with earlier and greater desynchronisation in the experienced tennis players. In particular, only experienced players showed desynchronisation in the high mu (11–13 Hz) band. No group differences were found in posterior alpha components. These results show for the first time that expertise differences during action observation and anticipation are unique to sensorimotor sources, and that no expertise-related differences exist in attention modulated, posterior alpha sources. As such, this paper provides a much cleaner measure of the human mirror system during action observation, and its modulation by motor expertise, than has been possible in previous work.

1. Introduction

The extent to which future events can be predicted is a key component of situational awareness that can support skilled performance (Endsley, 2000, 1995). Being able to infer the actions of others is crucial for effective interactions in dynamic environments, such as interception of a moving target (Wilson and Knoblich, 2005; Zago and Lacquaniti, 2005). Sport represents an ideal testing ground in which to study the neurophysiology of human action prediction systems that are developed with expertise (Makris, 2014). In comparison to less experienced performers, experienced athletes have an extremely well developed repertoire of domain-specific actions and a superior ability to successfully anticipate the actions of opposing players based on movement kinematics (Rowe and McKenna, 2001; Savelsbergh et al., 2002; Williams et al., 2011). For example, experienced tennis players are able to anticipate the direction of an opponent's shot from a wide range of postural cues and the dynamic positioning of the racket arm and the trunk (Cañal-Bruland and Williams, 2010; Huys et al., 2009; Williams et al., 2009).

Prediction of the outcomes of others' physical actions may be facilitated by a human mirror neuron system. This system is a network of brain structures that activate during both the execution and observation of goal-directed actions (Buccino et al., 2004; Molenberghs et al., 2012). The human mirror system has been argued to serve a role in understanding the intentions of other people's actions by using internal motor representations to form a generative model of how an action is performed to predict the outcome of the observed kinematics of others (Kilner, 2011; Kilner et al., 2007; Neal and Kilner, 2010; Rizzolatti et al., 2014). The mirror system may facilitate superior anticipation ability in athletes (Balser et al., 2014b; Wright et al., 2013, 2011, 2010). For example, superior anticipation ability in professional basketball players is associated with greater activation of the motor cortex during observation of basketball free throws (Aglioti et al., 2008).

There is evidence that mirror system activity can be indexed using EEG by measuring event-related power changes in mu (8–13 Hz) and beta (15–25 Hz) cortical sensorimotor oscillations (Pineda, 2005). Both the above changes are believed to be generated primarily in the

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pre-motor cortex (Babiloni et al., 2015; Meirovitch et al., 2015); a known mirror system region, as shown by a meta-analysis that found the pre-motor cortex to be one of several regions that reliably activated during both the execution and observation of actions (Molenberghs et al., 2012). Furthermore, ~10 Hz and ~20 Hz event-related desynchronisation (ERD) occurs during both the execution and observation of goal-directed actions, supporting the hypothesis that they represent mirror system activity (Fox et al., 2016; Järveläinen et al., 2004; Muthukumaraswamy et al., 2004; Muthukumaraswamy and Johnson, 2004). Mu activity can be divided into functionally specific subtypes. During the execution of different movement types, low frequency mu (8–10 Hz) shows a widespread movement-type non-specific activity pattern, which was suggested to be indicative of a somatotopically non-specific activation, and related to more general attentional processes (Pfurtscheller et al., 2000). Higher frequency mu (11–13 Hz) on the other hand shows a focused, movement-type specific pattern suggesting activation of somatotopically specific cortical networks (Pfurtscheller et al., 2000) during goal directed movements (Fumuro et al., 2015). Thus far, researchers have only focused on action execution, however on the basis of mirror system principles it would be predicted that these findings should be found in observation tasks. Furthermore, while beta activity is believed to play a similar functional role to mu, some researchers have suggested that beta activity is related to movement planning and preparation, whereas the primary function of mu is attentional allocation towards biological motion stimuli (Brinkman et al., 2014).

We investigate whether the degree of motor expertise one has in a real-world skill modulates mirror system activity during action observation. We investigated this question by comparing mirror system activity in experienced athletes and less experienced novices on a sport-specific action observation and anticipation task. Previously, research on expert dancers has shown greater mu and beta ERD in experts compared to novices during action observation (Orgs et al., 2008). Relatedly, other work has examined 8–10 Hz mu ERD during the observation of table tennis shots in participants of varying levels of expertise. Experienced players had significantly greater 8–10 Hz ERD when compared with less experienced and non-players (Wolf et al., 2014). However, in these two studies the authors averaged power values over large 1 s bins, meaning that fine-grained statistical analysis of group differences over time was not possible.

Typically, mirror system activity has been assessed using EEG channel data from electrodes positioned over sensorimotor areas (e.g. C3 and C4). However, due to volume conduction effects, there is no guarantee that activity recorded at the scalp electrode will have been generated in the cortical region directly under the electrode. This measurement issue is further complicated by the fact that mu oscillations occur in the same frequency band as posterior alpha (8–13 Hz) activity, and it has been shown that putative mu activity can become contaminated with non-mu alpha activity (Braadbaart et al., 2013; Perry et al., 2010). While task design can help reduce potential non-mu alpha contamination (Hobson and Bishop, 2016), the fact remains that EEG electrodes record activity from a mixture of sources, leading to doubts that activity recorded from sensorimotor electrode sites are exclusively measuring the activity of the mirror system, and may simply reflect differences in attentional focus (Perry and Bentin, 2009). The implication for research into expertise related differences in mirror system activation using mu ERD measures is that differences could be due to greater attention in experienced groups, rather than greater use of the mirror system.

Blind source separation techniques, such as independent component analysis (ICA), may offer a potential solution to this problem. ICA is widely used for separating artefacts from scalp-recorded EEG data (Jung et al., 1998), and is becoming increasingly popular as a technique for separating and studying independent brain processes (e.g. Gramann et al., 2010; Makeig et al., 2002, 2004). ICA identifies temporally independent signal sources in multi-channel EEG data as well as their pattern of projection to the scalp surface. Component scalp maps have been shown to be dipolar, and as such many EEG components have scalp maps that closely match the projection of a single equivalent dipole in the brain (Debener et al., 2005b; Delorme et al., 2012; Onton et al., 2006). The location of this dipole can then be estimated within a standard head model such as that of the Montreal Neurological Institute (MNI), giving a better spatial estimate of where component activity is being generated. Therefore, ICA can be used to separate sensorimotor mu from posterior alpha into distinct components (Makeig et al., 2004). Further analysis of component ERD could then be performed on the component corresponding to sensorimotor mu activity that will be free of contamination from activity originating in other cortical regions, allowing for a more precise estimate of hMNS activity.

By taking an ICA approach, the current work uses a novel method to investigate the role of cortical sensorimotor oscillations in facilitating the anticipation of actions in experienced and less experienced tennis players. To our knowledge no researchers have directly compared changes in high and low mu activity during action observation and anticipation in groups with differing levels of skill and experience with the actions being observed. We chose tennis as the vehicle to address the main questions because groundstrokes provide a very clear ‘critical period’ at which an occlusion can be made (at racket-ball contact) to assure only kinematic cues are available to participants. Furthermore, other researchers have used neuroimaging to successfully investigate expertise differences in neural activity using tennis stimuli (Balser et al., 2014a, 2014b; Cacioppo et al., 2014).

We hypothesized that during action observation prior to anticipation, experienced and less experienced players would engage in different cognitive strategies, with experienced players using their own motor expertise to aid in the understanding of the opponent's intention. In contrast, the less experienced participants would not have the observed motor acts in their repertoire, so would not be able to rely on their own motor expertise to derive action intention. This difference in processing would be reflected by earlier and greater mu and beta ERD in the experienced group, compared to the less experienced group. A secondary hypothesis was that group differences would arise differently in the low and high mu frequency band. As low mu is related to a general movement activity and allocating attentional resources to motion, both the experienced and less experienced groups were predicted to show ERD. In the high mu band, only the experienced group was predicted to show ERD because this activity is related to the access of movement-specific knowledge (Fumuro et al., 2015) which will be available to the experienced group but not to the less experienced novices.

2. Methods

2.1. Participants

Altogether, 18 experienced tennis players (6 females, M_{age}=21.12, SD=3.16) were recruited from local university tennis teams. The experienced players reported an average of 12.94 (SD=4.34) years of tennis experience, playing on average 7.65 (SD=4.08) hours per week, and had received formal instruction for an average of 8.06 (SD=2.95) years. Moreover, 21 psychology undergraduate students were recruited from the lead institution (14 females, M_{age}=22.60, SD=6.63) as less experienced participants. This latter group reported an average of 1.70 (SD=3.05) years of tennis experience, playing on average 0.90 (SD=1.29) hours per week, with an average of 0.90 (2.31) years of formal instruction. All participants self-reported playing right-handed. As a result of high levels of noise during the recording period, data from two participants (one experienced and one less experienced) were unable to be used in the EEG analysis. Therefore, for the EEG analysis, the total sample size was 37 (17 experienced players, 20 less experienced novices).