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

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).

2.2. Materials

The anticipation video was filmed using a tripod mounted Panasonic HC-X920 camcorder. The video was initially recorded at 1920×1080 pixels, reduced to 854×480 pixels during editing due to computational limitations. The video was recorded at 25 frames per second with a 16:9 aspect ratio. The camera was positioned on the 'T' where the centre service line meets the service line. The video footage was edited using iMovie 11 (Apple Inc., USA). Two skilled left-handed players featured in the video. One player was a qualified Lawn Tennis Association (LTA) Level 4 'senior performance' coach, defined as being able to coach national level players. The other player was a qualified LTA Level 2 coaching assistant, defined as being able to coach adult beginner players (https://www.lta.org.uk/coach-teach/coach-development/coaching-pathway/). Two left-handed coaches were employed for recording the stimuli as they were the only two members of coaching staff of sufficient expertise available at the tennis centre where the stimuli were recorded. The incongruence between the handedness of the players used for the stimuli and the handedness of the participants is unlikely to affect hMNS activity, as other studies have shown motor representations activated during action observation are effector independent (Sartori et al., 2013).

For the recording, one of the players stood positioned on the back line of the court and was fed balls by the second player, who was out of sight of the camera. The position of the camera meant that shots were filmed approximately from the point-of-view of an opponent player positioned on the service line (Fig. 1). The player being filmed performed both forehand and background groundstrokes while remaining at the back of the court. The players were instructed to perform prototypical shots clearly aimed to the left or right hand side of the court. Each player was recorded hitting 200 shots. The total of 400 shots contained a mixture of forehand and backhand groundstrokes.

The video was segmented into individual shots. Two of the original blocks of fifty trials were removed due to balls hitting the tripod during filming, causing discrepancies within these blocks regarding the camera angle. Shots that hit the net were removed, as were shots where the ball landed in the tramlines (which had been noted by an observer during filming). Finally, each remaining clip was judged as to the final position of the ball. Any shots that went down the middle of the court, left the camera's field-of-view notably early, or were ambiguous regarding shot direction were removed. Once suitable shots had been identified, they were occluded 40 ms (1 frame) prior to racket-ball contact. This occlusion point was selected as previous research suggests the largest expertise difference occurs at this occlusion point (Rowe et al., 2009).

Two behavioural experiments were run (not reported) to identify trials that discriminated experienced and less experienced participants based on their anticipation accuracy. Based on this initial pilot, 176 trials were selected. The trials were presented on a PC monitor with the sound turned off. The experiment was controlled from a computer using a custom MATLAB (The Mathworks inc, USA) script designed using PsychToolbox 3 (Kleiner et al., 2007). For each trial, participants were required to indicate via key press which direction they predicted the ball would go. This response was recorded and used to calculate anticipation accuracy as the percentage of correct trials.

2.3. Procedure

Trials were presented on a 19 in. Viglen LCD monitor with a spatial resolution of 1280×1024 pixel display with a temporal resolution of 60 Hz. Participants conducted the task individually in a quiet, darkened room in a single session, sitting 57 cm from the monitor in a comfortable chair. In order to limit movement artefacts, participants were requested to remain as still as possible during data collection, and use the breaks provided to change their posture.

Participants gave informed consent and were instructed on how to perform the task. They were presented with 10 practice trials (using shots not presented in the experimental trials). The 176 experimental trials were split into 4 blocks of 44 trials each, with a break between each block. Each trial lasted 6 s (4 s baseline, 2 s event), with a 2 s inter-trial interval. The experimental session took approximately 30 minutes to complete. Once the experimental session had finished, participants completed a questionnaire regarding their handedness and tennis experience.

2.4. EEG data acquisition

EEG was recorded in an electrically shielded room using an ActiveTwo headcap and a Biosemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands). EEG data were amplified with a sampling rate of 2048 Hz, and stored using ActiView software (Biosemi, Amsterdam, The Netherlands). Data were collected from 128 channels using active Ag-Agcl tipped electrodes. Two additional electrodes, common mode sense (CMS), and driven right leg (DRL) replaced traditional reference and ground electrodes during recording. DC offset voltages were kept below ± 25 mV.

2.5. EEG preprocessing

Initially, data were downsampled to 512 Hz using Decimator software (Biosemi, Amsterdam, The Netherlands). All pre-processing was performed in EEGLAB (Delorme and Makeig, 2004), an open source toolbox for EEG data analysis in the MATLAB environment.

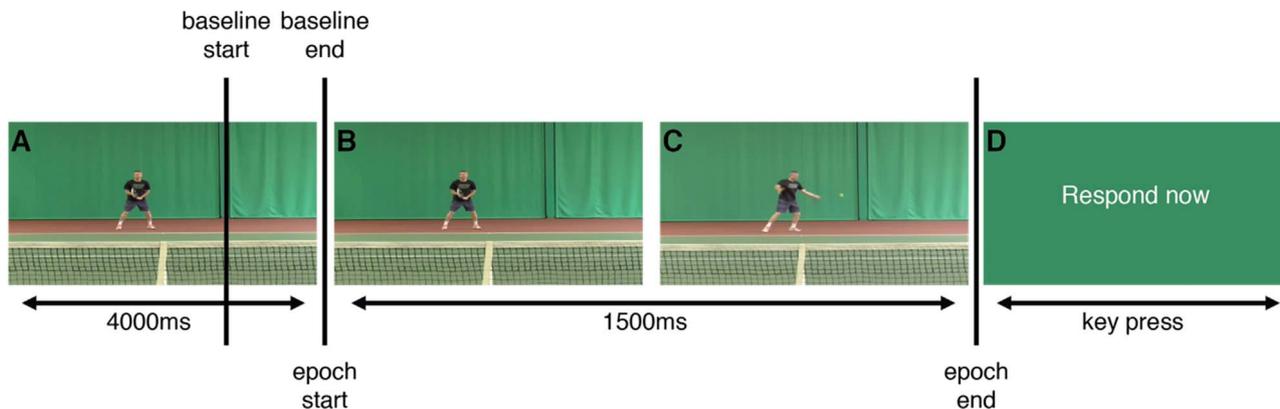Data were imported and referenced to the vertex electrode, and a

Fig. 1. An example of a single trial. A – Baseline period of 4000 ms showing a still image of the first frame of the trial video. B – Trial begins by video playing, each trial lasting approximately 1500 ms. C – Trial ends on the frame prior to racket-ball contact. D – Participants anticipate shot direction by key press. Epochs were time-locked to the video start, and lasted 1500 ms. The baseline period was 1000 ms prior to stimulus onset.

1 Hz high-pass filter was applied in order to remove low-frequency drift. Bad channels (exhibiting flatlining, evidence of electrode bridging, or excessive high-frequency noise), and non-eye blink (non-stereotyped high frequency noise) artefacts were removed manually from the continuous EEG data, with break event markers placed in the cleaned data to indicate where data had been rejected. The cleaned data was re-referenced to an average electrode. Independent component analysis (ICA) was then run on the cleaned, continuous EEG data (see below).

Epochs were created with the start of the video at 0ms. The epoch ended 1500ms post-stimulus onset. Any epochs containing break event markers were rejected. There was no difference between the experienced (M =150, SD=15.90) and less experienced (M=154, SD=12.38) groups in terms of total number of accepted epochs; t (35)=1.03, p=.31, d=0.28. The event period of the epoch captured the observation period while participants were watching the shot. The baseline period started at −1000 ms, and featured the still image of the first frame of the upcoming trial. An example epoch of stimulus presentation is displayed in Fig. 1.

2.6. Independent component analysis

The EEG data were decomposed into statistically maximally independent components (ICs) using the infomax algorithm in EEGLAB. The initial learning rate was set to 10E-4, and training was stopped when the learning rate fell below 10E-6. Following decomposition, an equivalent current dipole model was computed for each IC by using the DIPFIT Autofit routine in EEGLAB. Dipoles were localized within a three-shell boundary element model (BEM) of the Montreal Neurological Institute (MNI) standard brain. ICs that had a dipole with a residual variance smaller than 15% were selected for further analysis. This procedure led to an average of 18 components being selected per participant, and the groups did not differ in terms of number of ICs being selected; t (35)=0.51, p=.61, d=0.17. (Experienced; M=17.24, SD=6.89; less experienced; M=18.31, SD=5.56).

In order to facilitate group level analyses, all selected ICs were clustered based on their scalp map, dipole location, power spectrum, and event related spectral perturbation (ERSP). Clustering was performed within EEGLAB using the K-means algorithm, which produced clusters with the greatest possible distinction by minimizing variability within and maximising variability between clusters. ICs with a distance larger than three standard deviations from the mean of any cluster centroid were removed from the analysis. A total of 10 clusters were created. Each cluster was then inspected regarding the total number of participants contributing to a cluster, and the number of individual components that each participant contributed to a cluster. In cases where a participant contributed multiple ICs to one cluster, the IC whose dipole showed the lowest residual variance was selected (Grandchamp et al., 2012).

2.7. EEG data analysis

The main analyses were conducted on IC clusters (see Fig. 2). The event related spectral perturbation (ERSP) is a measure of average dynamic changes in amplitude of the broad band EEG frequency spectrum as a function of time relative to an experimental event (Makeig, 1993). ERSP in the 4–50 Hz frequency range was computed in EEGLAB using Morlet wavelet decomposition, applied over 200 overlapping windows, starting with a 3 cycle wavelet at the lowest frequency (Delorme and Makeig, 2004). The window size was 1115.23 ms wide, overlapped by 1105.815 ms, giving a time resolution of 9.415 ms. ERSP values were transformed into log-units and converted to decibel units (dB), by multiplying the log ratio with the factor 10 (Grandchamp and Delorme, 2011). Therefore, ERSP expresses the relative change in power during the event period in dB compared with the baseline (which in this case is the still video).

Baseline correction was conducted at the single trial level. Reduction power relative to the baseline is displayed in blue, with increases in power relative to the baseline displayed in red.

2.8. Statistical analysis

To assess for significant differences in ERSP time/frequency data between the experienced and less experienced groups, bootstrapped significance tests were performed. The potential for spurious significant findings being generated by multiple comparisons was controlled using the false discovery rate (FDR). The results of these tests are visualised on a time-frequency plot indicating points where significant differences at the $p < .01$ level arose. Each time/frequency plot presents data from a single independent component.

ERSP values averaged across both frequency band and time were also calculated. This process created a single baseline ERSP value, and a single event ERSP value. The overall ERSP value was derived by subtracting the event ERSP from the baseline ERSP (Pfurtscheller and Lopes da Silva, 1999). A negative ERSP value indicates overall power reduction (ERD) across the whole event compared to baseline, and a positive ERSP value indicates overall power increase (ERS). Group differences in ERSP values were calculated using two-way mixed ANOVAs, with group (experienced and less experienced) as a between-participants factor, and hemisphere (left and right) as a within-participants factor. The aims of this approach was to aid visualisation and to enable direct comparison with other published reports using the same procedure (e.g. Wolf et al., 2014).

3. Results

3.1. Behavioural results

There was a significant effect of experience level on anticipation accuracy, with the experienced players (M=60.94%, SD=6.83) responding significantly higher accuracy scores than the unexperienced players (M=48.52%, SD=5.97), t (37)=6.15, $p < .001$, d=2.01. There were no gender (p=.31) or age (p=.55) differences in accuracy.

3.2. Component clustering

From the 10 clusters computed, six were identified as reflecting clear brain processes, based upon the cluster properties (dipole location, scalp map, power spectrum, and ERSP). These clusters are displayed in Fig. 2. Sensorimotor clusters were identified based upon characteristic peaks in the power spectrum at ~10 and ~20 Hz. A distinct left and right sensorimotor cluster were found, and were distinguished by scalp maps showing projections to left and right central areas respectively. Dipole centroid locations were localised to sensorimotor areas (left sensorimotor Talariach co-ordinates: X=−19, Y=−13, Z=53, Brodmann area 6; Right sensorimotor Talariach co-ordinates: X=34, Y=0, Z=47. Brodmann area 6).

Other clusters reflecting brain processes were found. First, a frontal cluster showed low frequency theta (~4 Hz) and beta (~20 Hz) peaks in the power spectrum. The scalp map showed a frontal projection, with the dipole centroid located in Brodmann area 8 (Talairach co-ordinates: X=−12, Y=30, Z=38). Three separate clusters reflected ongoing non-mu alpha processes, and were identified based on a clear 10 Hz peak in the power spectrum. One posterior cluster was identified (Talariach co-ordinates: X=5, Y=−61, Z=27; Brodmann area 31). Finally, left (Talariach co-ordinates: X=−26, Y=−78, Z=−11; Broadmann area 19), and right (Talariach co-ordinates: X=26, Y=−79, Z=−10) occipital alpha clusters were found.

Of the four clusters not selected for further analysis (Fig. 2B), two reflected non-brain artefacts. These artefacts were judged based on the smoothly decreasing power spectrum and far frontal projection of the scalp map. The final two clusters showed scalp maps resembling
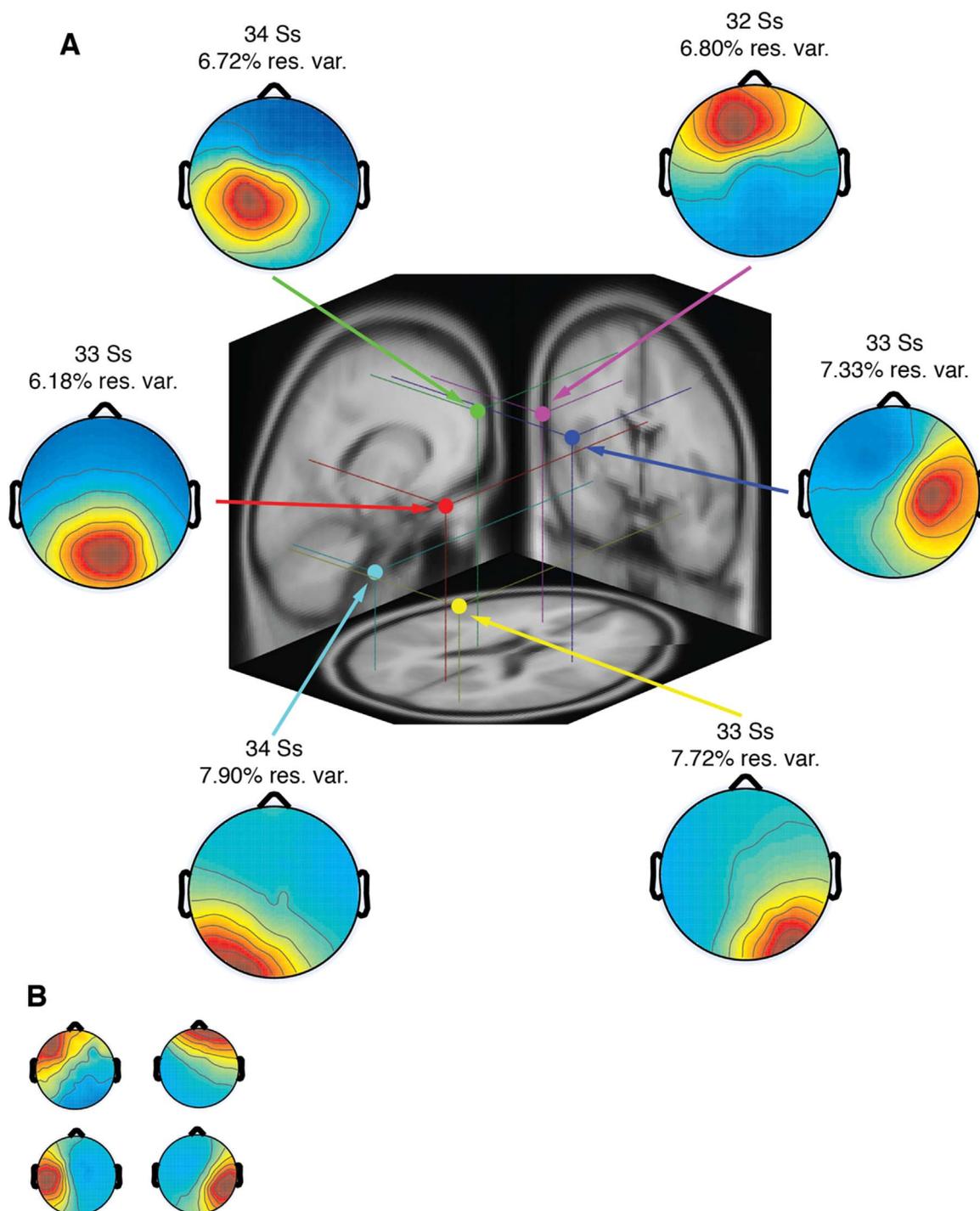
Fig. 2. A Dipole centroid location estimate for each independent component (IC) cluster within a three-shell boundary element model (BEM) of the Montreal Neurological Institute (MNI) standard brain. The projection of the dipole's electric field onto the scalp is shown in each scalp map. For each IC cluster, the number of participants (Ss) contributing to the cluster, and the mean residual variance (res. var.) are displayed above each scalp map. B Scalp maps for the four IC clusters not selected for further analysis. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

sensorimotor activity, however the dipole locations did not support a sensorimotor source. As it was unclear what brain process these clusters were related to, they were not analysed further.

3.3. EEG results

3.3.1. Group differences during action observation

It was hypothesized that during action observation, greater ERD in sensorimotor areas would be found in the experienced group when compared to the less experienced group. Figs. 3 and 4 display group differences in the two sensorimotor component clusters during action observation prior to anticipation. In the left sensorimotor cluster, bootstrapped significance tests showed that group differences arise relatively early in the epoch, with differences occurring approximately 100 ms post-stimulus onset (Fig. 3). In the right sensorimotor cluster, similar results were found, though group differences appeared to occur slightly later in the epoch (Fig. 4).

Across the whole epoch, ERD was greater in the experienced group. A two-way mixed ANOVA showed a significant main effect of group on mu ERD; $F(1, 30)=17.07$, $p < .001$, $np^2=.36$. ERD was greater in the
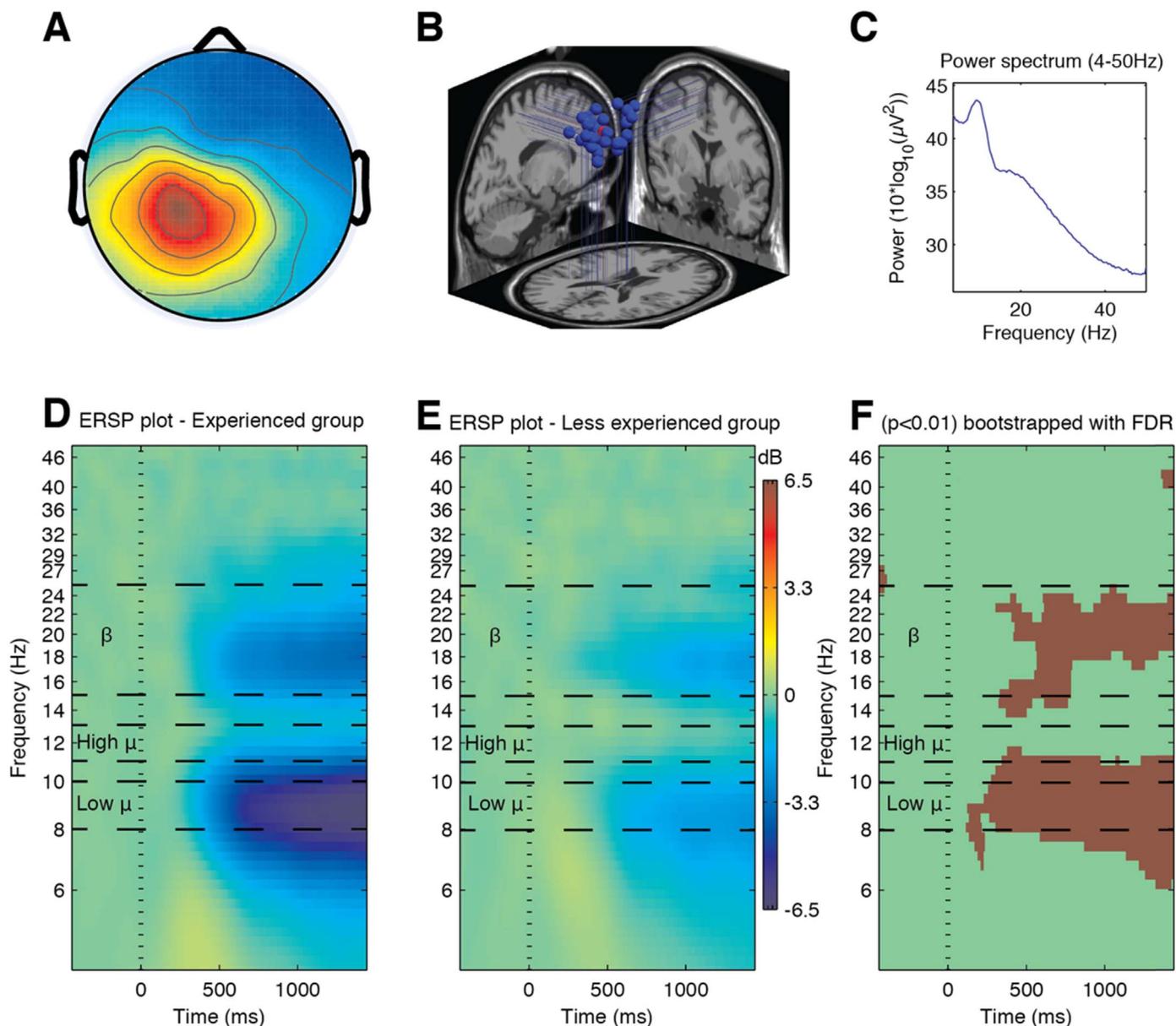
Fig. 3. Left sensorimotor component cluster. A Cluster scalp map. B Dipole locations for each participant contributing to the cluster, with the centroid location displayed in red. C Component cluster power spectrum (4–50 Hz). D-E ERSP time/frequency plots for experienced (D) and less experienced (E) groups. F Significant differences between experienced and less experienced group time/frequency plots at the $p < .01$ level, based on bootstrapped statistics with multiple comparisons controlled for with the false discovery rate (FDR). μ=mu, β=beta.

experienced group (Left hemisphere; M=−2.46 dB, 95% CI=−3.07 dB−−1.85 dB; right hemisphere; M=−1.11 dB, 95%CI= −1.54 dB−−0.68 dB), compared to the less experienced group (Left hemisphere; M = −0.68 dB, 95%CI = −1.55 dB–0.19 dB; right hemisphere; M=0.21 dB, 95%CI=−0.13 dB−−0.53 dB). There was also a significant main effect of hemisphere; $F (1, 30) = 8.62$, $p < .01$, $np^2 =.22$, with greater ERD found in the left (M=−1.67 dB, 95% CI=−2.48 dB −1.29 dB), compared to the right hemisphere (M=−0.49 dB, 95%CI= −0.83 dB−−0.15 dB). The group x hemisphere interaction was not significant; $F (1, 30)=0.85$, $p=.37$, $np^2=.03$. These results are presented in Figs. 5A, C and 6A, C.

In the beta band, there was a significant main effect of group on beta ERD; $F (1, 30)=23.56$, $p < .001$, $np^2=.44$, with greater ERD in the experienced group (Left hemisphere; M=−1.57 dB, 95%CI=−1.90 dB − −1.24 dB; right hemisphere; M=−1.01 dB, 95%CI=−1.24 dB−−0.78 dB), compared to the less experienced group (Left hemisphere; M=−0.71 dB, 95%CI=−1.08 dB−−0.34 dB; right hemisphere; M=−0.18 dB, 95%

CI=−0.38 dB−−0.02 dB). The main effect of hemisphere was significant; $F (1, 30)=9.48$, $p < .01$, $np^2=.24$, with greater ERD in the left hemisphere (M=−1.20 dB, 95%CI=−1.53 dB−−0.86 dB) compared to the right (M=−0.60 dB, 95%CI=−0.80 dB−−0.39 dB). There was no significant interaction effect; $F (1, 30)=0.14$, $p=.72$, $np^2=.01$. These results are presented in Figs. 5B, D, and 6B, D.

3.3.2. Differential activity in low and high mu frequency bands

Expertise-related differences in ERD of low and high mu activity were hypothesized. Visual inspection of the ERSP time/frequency plots (Figs. 3D−E and 4D−E) suggested there to be differences in activity in the low (8−10 Hz) and high mu frequency range (11−13 Hz) (Figs. 3D−E and 4D−E). These differences are shown in Figs. 5E−H and 6E−H.

In the low mu band, there was evidence of ERD in both groups, though the magnitude was greater in the experienced group. A two-way mixed ANOVA showed a significant main effect of group on low mu ERD across the whole epoch; $F (1, 30)=17.82$, $p < .001$, $np^2=.37$, with
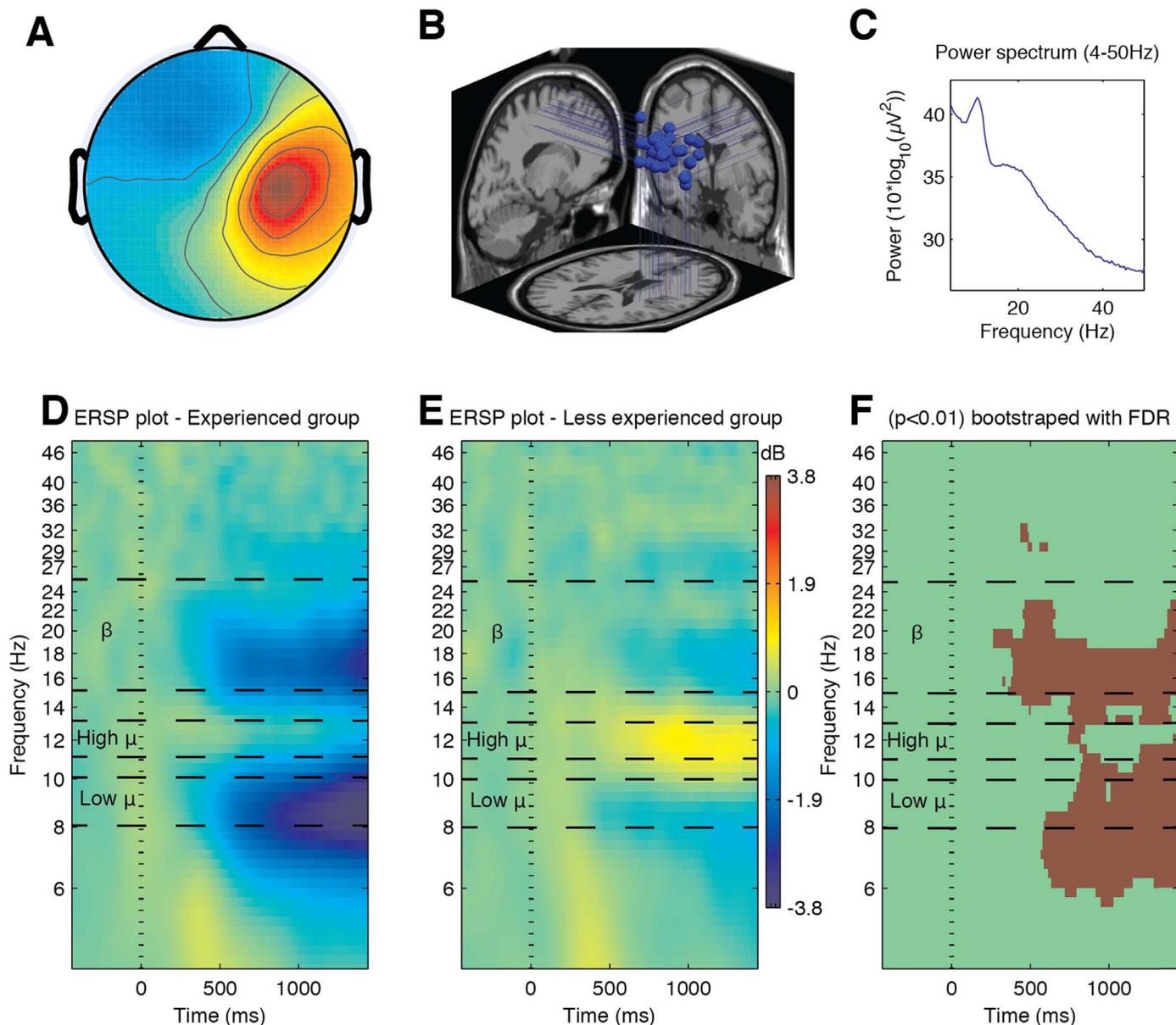
Fig. 4. Right sensorimotor component cluster. A Cluster scalp map. B Dipole locations for each participant contributing to the cluster, with the centroid location displayed in red. C Component cluster power spectrum (4–50 Hz). D-E ERSP time/frequency plots for experienced (D) and less experienced (E) groups. F Significant differences between skilled and less experienced group time/frequency plots at the *p* < .01 level, based on bootstrapped statistics with multiple comparisons controlled for with the false discovery rate (FDR). μ=mu, β=beta. (For interpretation of the references to color in this figure legends, the reader is referred to the web version of this article.).

greater ERD in the experienced group (Left hemisphere; M=−3.57 dB, 95% CI= -4.49 dB - -2.65 dB right hemisphere; M=−1.70 dB, 95% CI=−2.35 dB−−1.05 dB), compared to the less experienced group (Left hemisphere; M=−1.03 dB, 95%CI = -2.03 dB−−0.03 dB; right hemisphere; M=−0.04 dB, 95%CI=−0.44 dB−0.36 dB). There was also a significant main effect of hemisphere; F (1, 30)=10.29, $p < .01$, np^2=.26, with greater ERD found in the left (M=−2.46 dB, 95% CI=−3.37 dB−−1.54 dB) compared to the right hemisphere (M=−0.92 dB, 95%CI=−1.38 dB−−0.45 dB). The group x hemisphere interaction was not significant; F (1, 30)=1.81, p=.19, np^2=.06.

Only the experienced group showed evidence of ERD in the high mu band. A two-way mixed ANOVA showed there was a significant main effect of group; F (1, 30)=9.98, $p < .01$, np^2=.25, with greater ERD in the experienced group (Left hemisphere; M=−1.17 dB, 95%CI = −1.52 dB−−0.82 dB; right hemisphere; M=−0.43 dB, 95% CI=−0.69 dB−−0.17 dB), compared to the less experienced group who showed no evidence of ERD occurring (Left hemisphere; M=−0.27 dB, 95%CI = -1.00 dB - 0.46 dB; right hemisphere;

M=0.50 dB, 95%CI=0.18 dB−0.82 dB). The main effect of hemisphere was significant; F (1, 30)= 4.90, $p < .05$, np^2=.14, with greater ERD in the left hemisphere (M=−0.74 dB, 95%CI=−1.32 dB−−0.16 dB) compared to the right (M=0.01 dB, 95%CI=−0.27 dB−0.28 dB). There was no significant interaction effect; F (1, 30)=0.02, p=.90, $np^2 < .01$.

3.3.3. Group differences in other component clusters

ERSP plots for both the experienced and less experienced groups in other component clusters are displayed in Fig. 7. Bootstrapped significance testing did not reveal any significant group differences in ERSP between 4−50 Hz in any of the component clusters (all not significant at $p > .05$).

3.3.4. Channel analysis

In order to compare the findings reported here with existing literature, the same set of analyses as reported above was performed on channel data from electrodes C3 (positioned above left motor cortex) and C4 (positioned above right motor cortex), commonly used
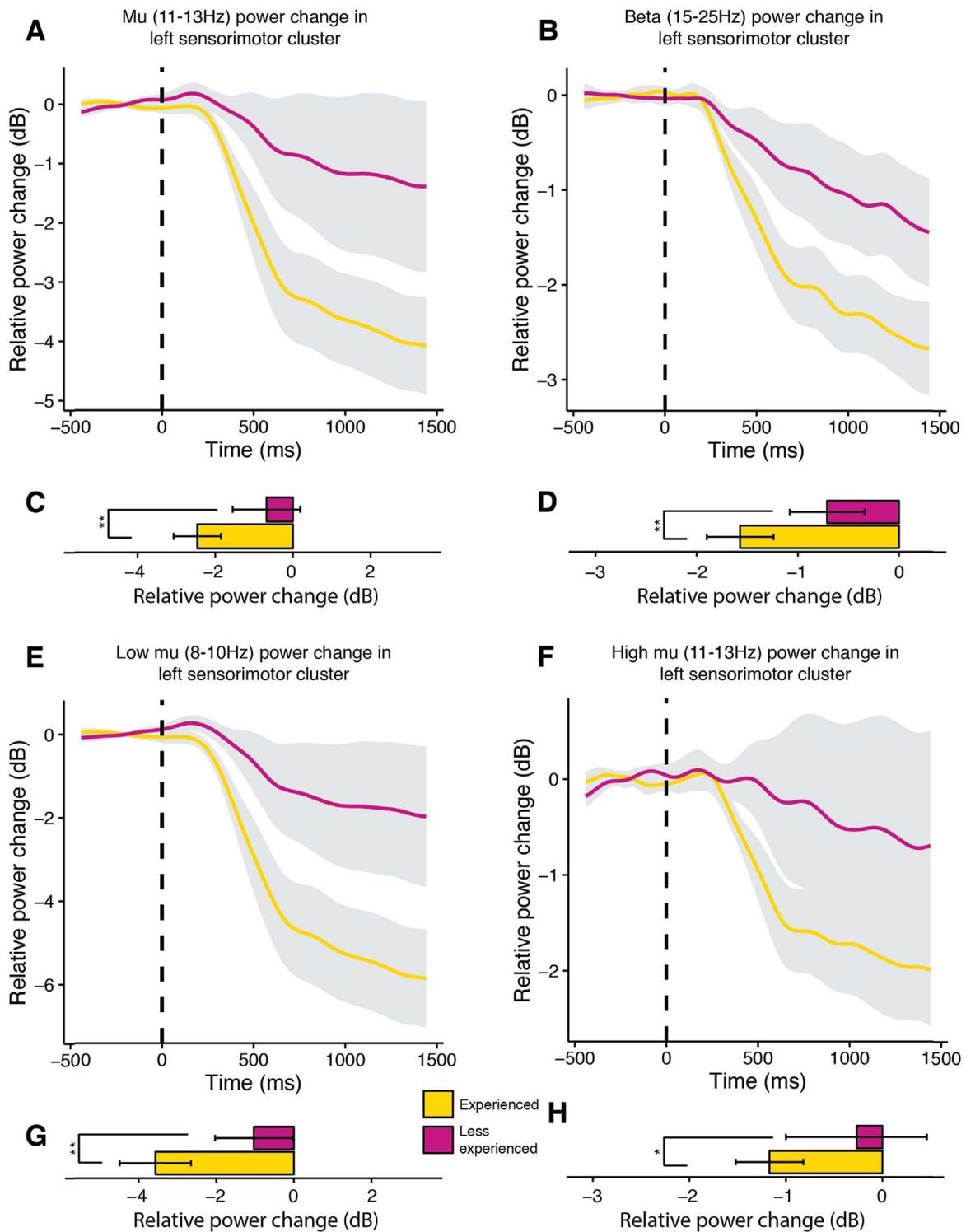
Fig. 5. Relative power changes in mu and beta bands in the left sensorimotor component cluster. A-B. Relative power changes in the mu (8–13 Hz) (A) and beta (15–25 Hz) (B) frequency bands. Shaded areas represent 95% confidence intervals. C-D Relative power changes over the whole event period relative to baseline in the mu (8–13 Hz) (C) and beta (15–25 Hz) (D) frequency bands. Error bars represent 95% confidence intervals. E-F. Relative power changes in the low mu (8–10 Hz) (E) and high mu (11–13 Hz) (F) frequency bands. Shaded areas represent 95% confidence intervals. G-H Relative power changes over the whole event period relative to baseline in the low mu (8–10 Hz) (G) and high mu (11–13 Hz) (H) frequency bands. Error bars represent 95% confidence intervals. **=p < .01, *=p < .05.

sites for investigating mu rhythm activity (e.g. Cannon et al., 2014; Wolf et al., 2014). All group based analyses produced similar results to those reported above indicating group differences between experienced and less experienced participants were apparent in both the EEG channel data and the independent components. These data are shown in the supplementary information.

4. Discussion

We examined differences in mirror system activity during sports-related action observation prior to making an anticipatory judgment in experienced and less experienced tennis players. We hypothesized that greater mu and beta ERD would be observed in experienced players during action observation, reflecting greater use of the mirror system.
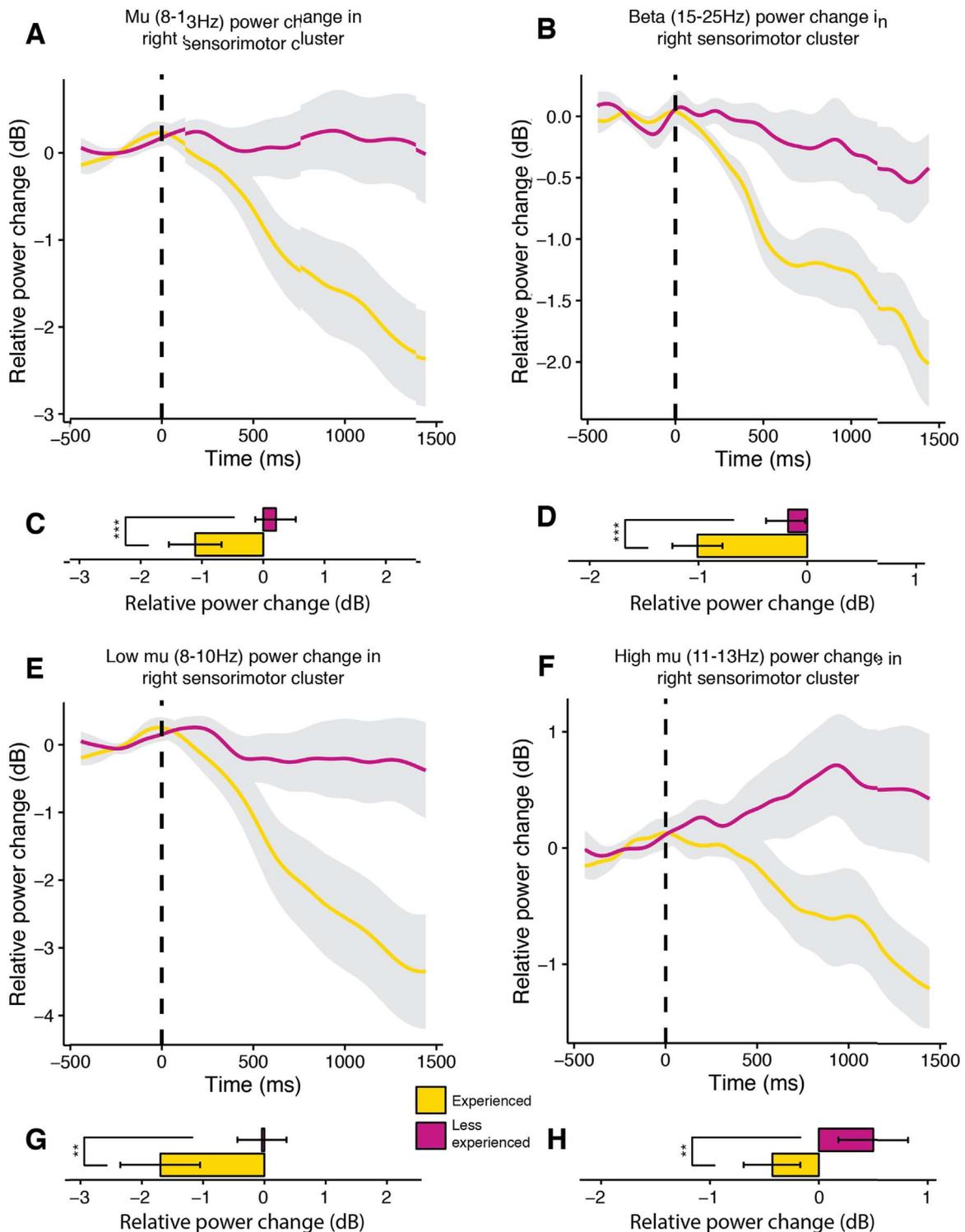
Fig. 6. Relative power changes in mu and beta bands in the right sensorimotor component cluster. A-B. Relative power changes in the mu (8–13 Hz) (A) and beta (15–25 Hz) (B) frequency bands. Shaded areas represent 95% confidence intervals. C-D Relative power changes over the whole event period relative to baseline in the mu (8–13 Hz) (C) and beta (15–25 Hz) (D) frequency bands. Error bars represent 95% confidence intervals. E-F. Relative power changes in the low mu (8–10 Hz) (E) and high mu (11–13 Hz) (F) frequency bands. Shaded areas represent 95% confidence intervals. G-H Relative power changes over the whole event period relative to baseline in the low mu (8–10 Hz) (G) and high mu (11–13 Hz) (H) frequency bands. Error bars represent 95% confidence intervals.***= p < .001, **=p < .01.

Behavioural results showed a large group difference in anticipation accuracy, providing construct validity and satisfying criteria for this test being informative on the processes that underlie skilled anticipation (Ericsson and Smith, 1991; Williams and Ericsson, 2005). As such, it was possible to investigate differences in neural activity between groups during the action observation period. The experienced group showed significantly greater ERD in both the mu and beta frequency bands during action observation, compared to the less experienced group. These results are in line with previous research (Aglioti et al., 2008; Balser et al., 2014b; Wright et al., 2013, 2011, 2010), and suggest a stronger perception-action coupling in the mirror system of experienced tennis players. This coupling may facilitate superior
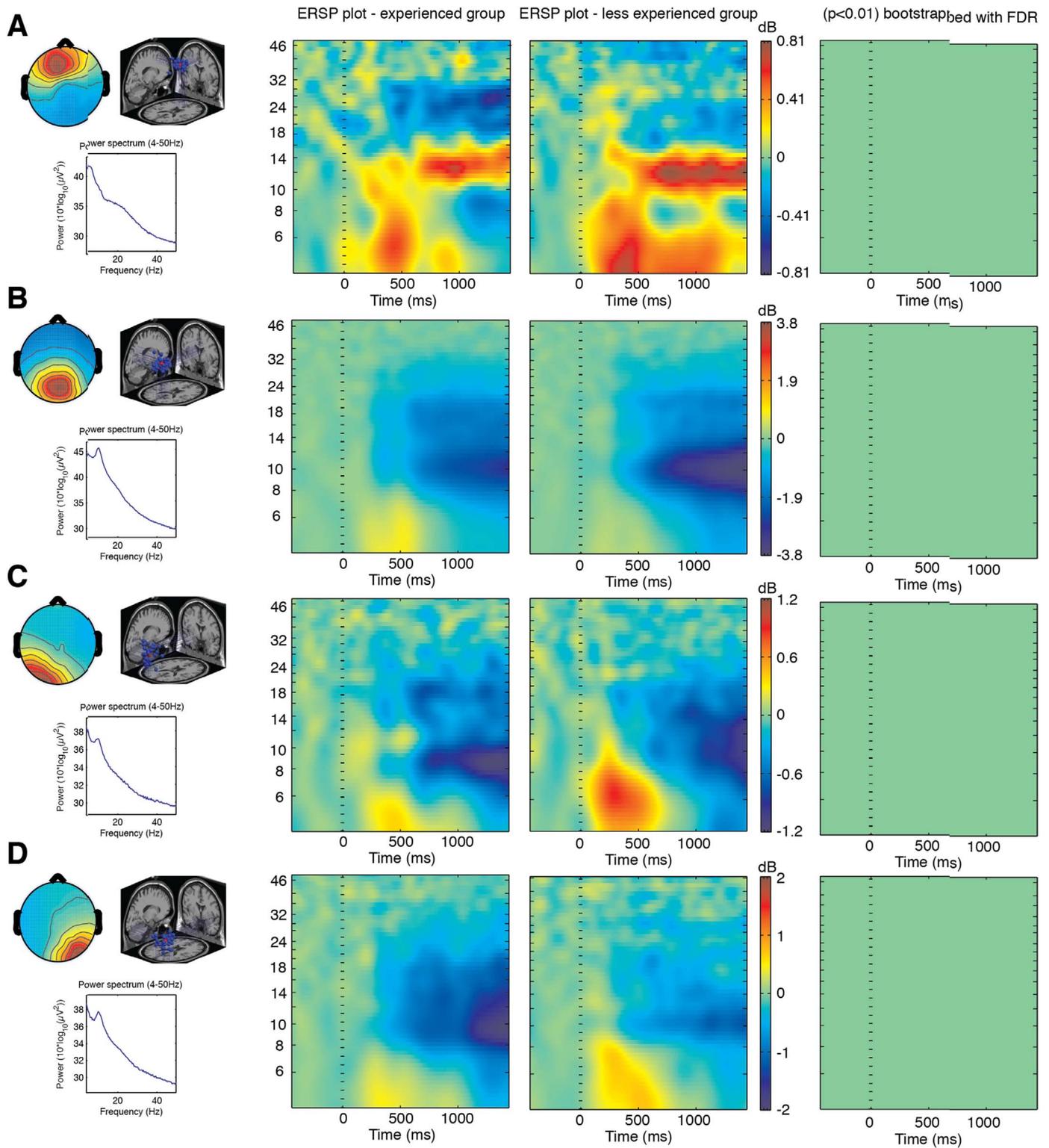
Fig. 7. Scalp map, dipole location, power spectrum, and ERSP for experienced and less experienced group for A frontal IC, B posterior alpha IC, C left occipital alpha IC, and D right occipital alpha IC.

anticipation ability.

We found that group differences were observed only in sensorimotor component clusters, and not in clusters that reflected parietal alpha or visual activity in the occipital cortex. This finding suggests that experience related differences in neural activity during this task were unique to sensorimotor areas. This finding also suggests that our results are not solely due to differences in attention between the two groups. If this were the case, it would be expected that significant group

differences would occur in other clusters showing a clear alpha component, as posterior alpha is modulated by attentional demand (Klimesch, 1999; Sauseng and Klimesch, 2008). Therefore, our results show that mu and beta activity from sensorimotor locations are key in distinguishing experienced from less experienced participants during action observation. Whilst this task did not find any evidence for a role of alpha ERD in action anticipation, it is plausible that group differences could emerge in a more challenging task. For example,

increasing task complexity e.g. by including more information on which to base the anticipation, or increasing the number of response options, may lead to greater alpha ERD in unexperienced participants as they begin to find the task more demanding. On the other hand, experienced player's would be able to cope with the increased demands, due to their domain specific expertise, and so would show less alpha ERD (Del Percio et al., 2009).

Only the experienced group showed overall ERD in the high mu band (11–13 Hz), with no ERD in the less experienced group. This difference could reflect the activation of specific motor representations in the experienced group, which are unavailable to the less experienced participants. This suggestion is supported by evidence showing that high mu activity indicates activation of somatotopically specific cortical networks, relevant to specific goal-directed actions being performed (Fumuro et al., 2015; Pfurtscheller et al., 2000). By extending those previous findings into action observation in the present work, our finding implies that experienced players were able to access their specific motor representation for the shot being observed, and use this to understand the information present in the kinematics.

In the low mu band (8–10 Hz), significantly greater magnitude of ERD was observed in the experienced group. During action execution, low mu is believed to reflect general attentional processes and non-specific motor behaviour. Relating this to action observation, ERD in the less experienced group would be expected as they are still able to process biological motion for an action without having specific motor expertise. It is possible then that low mu ERD in the less experienced group reflects general orientation to, and recognition of, biological motion. Even so, the experienced group still showed greater ERD, implying that they possess greater knowledge of general movement patterns (Romeas and Faubert, 2015).

Differences in the beta band appeared similar to the mu band, with a greater magnitude of ERD in the experienced group. Whilst these results do not point to any clear differences between mu and beta activity, one possibility is that beta activity indexes the degree of uncertainty in the participants' understanding. Recent published reports suggest that beta band activity plays a role in the execution of forward models (Palmer et al., 2016). These are internally generated motor models that estimate the end outcome of an action faster than is possible by external feedback (Kilner et al., 2007; Miall, 2003; Wolpert and Miall, 1996), and have been hypothesized to allow for the anticipation of another's action (Yarrow et al., 2009). For instance, research into motor preparation found the amount of uncertainty of an action's goal affected the degree of beta power changes, with greater ERD associated with greater response certainty (Tzagarakis et al., 2015, 2010). It may be that greater beta ERD in the experienced group reflects greater certainty as to the outcome of the action being observed, due to their superior motor expertise. It is worth noting that the level of uncertainty is this task was relatively low. As the anticipation task required a selection between two outcomes, there was a 50% chance of guessing correctly. Therefore, greater group differences between experienced and less experienced athletes may become apparent in a task where a greater number of response options are available. It would be expected that experienced players should still show a higher degree of certainty due to their superior ability to understand their opponent's intention. Unexperienced players would however become less certain as the chances of guessing correctly are reduced.

Group differences in the beta band appeared clearer in the analysis on ICs compared to the channel analysis (see supplementary materials). One possible explanation for this is that the IC analysis has improved source separation capability compared to analyses based on EEG channels. In the channel data, volume conduction makes it possible that beta activity recorded at the central electrodes could have multiple different generator sources. If group differences only occur in sensorimotor areas, these differences may be obscured by beta activity generated by different sources, which do not differ between groups.

When using the ICs for analysis, it assures that only beta activity generated from a sensorimotor site is analysed. Therefore, a cleaner measure of sensorimotor generated beta activity is analysed, making group differences clearer. Other work has shown that analysis of ICs can provide a clearer measure of neural activity than analyses of EEG channel data (e.g. Debener et al., 2005a).

Despite the use of ICA, source localisation with EEG is imprecise, only providing an estimate as to the generator of the activity. As such we were unable to determine whether mu/beta activity arose in the motor or sensory cortex. However, dipole location estimates for the two sensorimotor clusters analysed here do correspond to the findings of fMRI studies that have shown sensorimotor areas to exhibit greater activations in experienced athletes (Balser et al., 2014b; Wright et al., 2013, 2011, 2010). It is important that researchers work to further improve the accuracy of the localisation of mu and sensorimotor beta activity, and simultaneous EEG-fMRI may be one way of achieving this (Huster et al., 2012). Although precise source localisation was not possible in the current study, precision was sufficient to clearly distinguish and separate sensorimotor locations from posterior and occipital locations.

We examined mirror system activity during action observation, but did not have an action execution condition. It may be that the neural activity during action observation would differ if subsequent execution is required to respond to the observed action. While such a design was not possible here, due to movement artefacts that would be present in the EEG data, such studies remain an important area for future research (Walsh, 2014). Recent advances in mobile brain/body imaging (Gramann et al., 2011), and mobile EEG applied to sport (Park et al., 2015), may make such studies possible in the future.

One issue when studying real world experts is that it is not possible to fully dissociate motor expertise from visual familiarity. As a function of their expertise, the tennis players recruited will have developed highly defined motor plans required for playing tennis at a high level. They also will have a high degree of visual familiarity of observing tennis shots. Other researchers have shown the mu and beta activity during action observation are not modulated by the amount of visual familiarity one has (Cannon et al., 2014). Furthermore, researchers comparing experienced players with experienced 'watchers' (such as spectators, referees, and coaches) have shown that only players are able to use motor-specific knowledge to anticipate, and show higher accuracy than experienced watchers (Aglioti et al., 2008; Williams and Davids, 1995). These findings make it unlikely that our results are due to differences purely in visual familiarity between the two groups. As such, our results suggest that experienced tennis players are able to use their own motor expertise and activate stored motor representations of specific actions being observed, that then may play a role in aiding the accuracy of subsequent anticipation.

We have shown that neural activity in sensorimotor areas occurs during the observation of other people's actions, supporting the theory that areas involved in executing actions are also activated during action observation. Furthermore, we report that the level of expertise one has in the observed action modulates this sensorimotor activity. We extend the findings of previous work by using ICA, to show for the first time that these expertise differences are unique to sensorimotor sources, and that no expertise-related differences exist in attention modulated, posterior alpha sources. As such, we provide 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. Whilst tennis was the specific domain studies here, we predict that similar processes underlie skilled anticipation both in other similar sports and dynamic real-world contexts.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuroimage.2016.10.022.

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