RESEARCH ARTICLE

Predicting the fate of basketball throws: an EEG study on expert action prediction in wheelchair basketball players

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Abstract

The ability to anticipate and detect changes in human movement helps people to modify their behaviors in ever changing environments. Studies indicate that expertise modulates observation of domain-specific actions in sports—a process that is crucial for adapting rapidly to a new situation, often before awareness of environmental changes is achieved. Here, we explored the electrophysiological underpinnings of wheelchair basketball players predicting the fate of free throws performed by wheelchair basketball athletes. We performed electroencephalography (EEG) in semi-professional wheelchair players with different degrees of expertise (players) and in ambulant, non-expert people (controls) while they observed movie stimuli of a free throw that could land inside or outside the basket. On each trial, participants were asked to predict the outcome of the throw. For each group, event-related potentials (ERPs) were averaged as a function of condition, using only the trials that were correctly predicted. Results show that compared to controls, expert players exhibit a greater negative amplitude of oCNV over Pz (an observational contingent negative variation-like waveform which is considered a marker of action effect prediction) during the wrist movement preceding the ball release (the last 100 ms of the shot), which carries the most crucial kinematic information regarding the fate of the throw. Our data provide further support to the view that functional modulation of the action observation network is associated with expertise.

Keywords EEG · Expertise · Action prediction · Action observation

Introduction

When we observe our surroundings, we predict what will happen next. We use this information to understand outcomes and update our own position, intention, or behavior. Ultimately, predicting the next moment helps us to form an accurate representation of our social surroundings. Depending on our previous experience as well as the characteristics of the surroundings, an individual generates expectations

and focuses on different internal and external cues to successfully predict the next event (Heil et al. 2018; Aglioti et al. 2008). For experts in sports and music, body kinematics can be even more informative than other environmental factors that unfold around them (Calvo-Merino et al. 2006; Tomeo et al. 2012; Urgesi et al. 2012; Makris and Urgesi 2013; Candidi et al. 2014; Weast et al. 2014). In this study, we explore the electrophysiological signatures of domain-specific action observation in wheelchair basketball athletes with different degrees of expertise. In particular, we focused on the event-related potential (ERP) waveform during the kinematically informative moments of a free throw.

When we observe actions, the action observation network (AON) becomes involved (Hardwick et al. 2018). This network comprises premotor and inferior parietal regions that are also activated during action execution. Findings suggest that action observation is supported by our own motor capacities; for instance, TMS studies show corticospinal facilitation of the hand muscles measured via motor-evoked potentials when observing grasping pictures with implied motion (Urgesi et al. 2006). It has also been suggested

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that anticipating the actions of another person might rely on a finely tuned and partially implicit perceptual mechanism (i.e., an inner motor simulation process) supported by embodiment and predictive coding (Abreu et al. 2017). At the electrophysiological level, ERP evidence from the parietal electrodes, specifically a negative deflection, has been associated with action effect prediction (Hughes and Waszak 2011; Jin et al. 2011; Savoie et al. 2018). Related to this, a slow negative deflection over fronto-central regions, the so-called contingent negative variation (CNV), has been proposed to reflect cue-initiated motor response preparation (Gomez et al. 2003), with variations in amplitude and topography due to task requirements (Rohrbaugh et al. 1976). CNV has been generally proposed to reflect the retrieval of a motor program from memory, and the late CNV (lCNV) to reflect sensory anticipation as well as movement preparation (Bender et al. 2004). The lCNV is thought to be involved in both low- and high-level planning processes (Zaepffel and Brochier 2012). Kourtis et al (2010; 2013) showed that the CNV waveform pattern corresponds to the planning period of a partners' action in a joint action task, suggesting that motor simulation might occur for observation and anticipation of an action. Overall, the evidence suggests that our own movement capacities influence action anticipation and that it might be reflected in the CNV waveform. For ballet dancers, this enhancement can be shown while they watch dance moves compared to novice groups (Di Nota et al. 2017). Crucially, for the present study, there is evidence that elite basketball players can predict successful free throws more rapidly and accurately based on cues from body kinematics, as reflected by a difference in corticospinal facilitation between experts and novice groups during the observation of successful and unsuccessful basket shots (Aglioti et al. 2008). Unlike amateurs, expert basketball players can detect deception from kinematics and postural cues (Fujii et al. 2014; Sebanz and Shiffrar 2009), and when a part of the body kinematics is disguised, it reduces the experts' accuracy to the level of amateurs (Rowe et al. 2009). Furthermore, studies on ERPs show a larger N400 during the perception of incorrect execution in basketball players but not in naïve controls (Proverbio et al. 2012), with similar results found in expert dancers (Orlandi et al. 2017). Complementary findings suggest that differences in neural activity related to experience can be unique to sensorimotor areas: expert tennis players have a greater accuracy in anticipating the outcome of tennis-related actions and greater event-related desynchronization in *Mu* rhythm (8–13 Hz) and beta (14–30 Hz) frequency bands, associated with activation of the AON (Denis et al. 2017). In a sport-specific attentional cueing task, CNV has also been found during action observation in the context of expertise (Wang and Tu 2017). Accumulating information from different samples of population and expertise converges toward the evidence that AON processes are imperative to

understanding how predictive processing works. In the current study, we focused on wheelchair basketball athletes.

Wheelchair basketball, just like standard basketball, is an open-skill sport where the environment changes constantly and it requires rapid adaption and response flexibility in disabled athletes (Di Russo et al. 2010). In wheelchair basketball, athletes are functionally classified from one (most severe disability) to four (least severe disability) according to the level of trunk movement and stability (De Lira et al. 2010; Maynard et al. 1997). During competition, the functional classification of the players is balanced to achieve comparable levels of physical ability across the competing teams, as the ability to throw a ball from a wider range of distances and upper arm circumference are related to success in scoring (Cavedon et al. 2015; Malone et al. 2002). Players are required to be exceptionally strong and able to recover from harsh falls as well as to adapt quickly to the demands of the game. Their expertise moves beyond their respective injuries, especially for an action such as a free throw (which requires movement mainly from the upper body).

Our paradigm focused on action prediction from body kinematics and investigated the electrophysiological correlates of action anticipation in expert wheelchair athletes. We expected the neurophysiological signals of action observation to be modulated by basketball expertise, specifically at the most informative moments of a basketball free throw kinematics, as shown by previous research (Abreu et al. 2012). Moreover, we expected the signals to be modulated by the fate of the basketball shot (i.e., whether it was successful or unsuccessful). To test this, we asked players from the Santa Lucia wheelchair basketball team to observe movies of another player and predict the outcome. We tested expert wheelchair basketball players, amateur wheelchair basketball players and naïve walking controls to investigate how specific motor handicap and motor expertise might impact motor prediction and the electrophysiological markers that accompany such expertise. To the best of our knowledge, this study is the first attempt to investigate how motor expertise might impact prediction of the consequences of a motor action and the electrophysiological markers that accompany such expertise.

Methods and analysis

Participants

The study was approved by the local Ethics Committee at the Fondazione Santa Lucia Research Hospital (Rome, Italy) and followed the ethical standards of the 1964 Declaration of Helsinki. The sample consisted of 16 players, recruited from the Santa Lucia Wheelchair Basketball Team in Rome. Sixteen expert

players (male, age: mean = 28.94, ± SD = 9.51; expertise: mean = 9.14, ± SD = 9.59; years since injury: mean = 18.86, ± SD = 10.11) were tested.

The players comprised athletes who actively took part in matches of the "Serie A1", the highest level of the Italian Wheelchair Basketball Championship, within the Italian Wheelchair Basketball Federation (FIPIC), and athletes within the "Serie B", with less years of experience compared to "Serie A1".

All players had deambulation issues and were full-time wheelchair users with reasons ranging from thoracic-back injury, paralysis, or amputation of two limbs. The only exception was one participant who could walk short distances with the aid of crutches, and another who could walk with prosthetic legs.

24 control participants were recruited from La Sapienza, University of Rome. Three participants were excluded due to an accuracy below 55%, and four more were excluded due to technical failure to send triggers; therefore, EEG analyses were conducted on a total sample of 17 basketball naïve control participants (7 male, 10 female; age = 26.4, SD = 5.99) and 16 wheelchair basketball players. One player was left handed. All participants had normal or corrected-to-normal vision and did not report head traumas or psychiatric disorders.

Stimulus selection

The movie stimuli consisted of movie recordings of a wheelchair basketball player (Point 1) of the Santa Lucia Wheelchair Basketball Team (Fig. 1b). The movie stimuli were recorded from a sagittal viewpoint and displayed the shooting execution up to the first frame of the ball leaving the hand. In these stimuli, it was possible to observe and discriminate clearly between a shot that would or would not be successful for both experts and completely naïve participants. Therefore, the movies were in principle adept at highlighting different neurophysiological signals associated with expertise, while providing a comparable number of accurately perceived trials between each group.

The movement of the actor started, on average, 789 ms before the movie stimulus ended (SD = 170.9). The natural execution of the throw itself lasted approximately 80 ms (SD = 22.6), where the player extended the arm, closed the wrist and let go of the ball. During the baseline part of the movie stimuli (mean = 1105.5 ms, SD = 185 ms), the player was seated on a wheelchair with the ball at hand with a slight rocking movement. The baseline part of the movie stimuli was validated to make sure that the kinematics were uninformative by asking eight naïve participants to try to guess the outcome of the actions. The pilot participants performed at chance level and with no significant difference
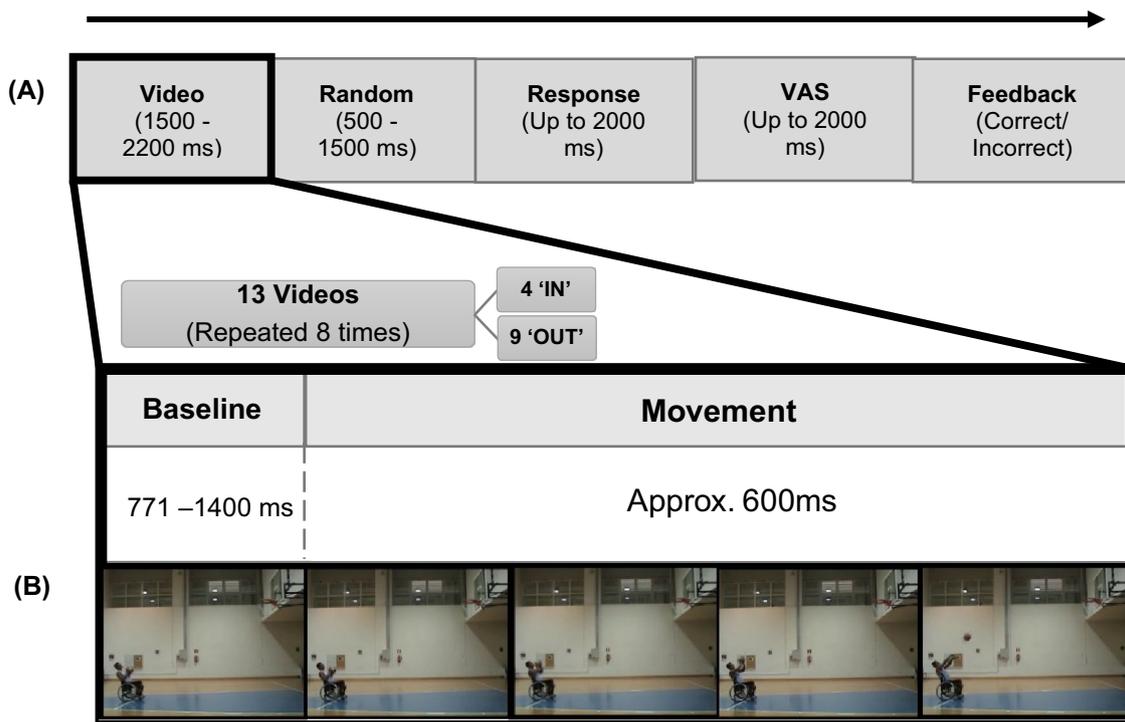

Fig. 1 a Timeline. (**b**) Procedure: a representation of the movie progression, first, middle and last frames of the movie (1st frame—the player sits still; 2nd frame—the player initiates the movement; 3rd frame—the player moves to execute the throw; 5th frame—the movement is completed when the player's wrist is closed and the ball is let go)

between the likelihood of correct response for either condition (Mean$_{IN}$ = 42.3%, SD$_{IN}$ = 22.3; Mean$_{OUT}$ = 51%, SD$_{OUT}$ = 24.4; $\chi(1)$ = 0.989, p = 0.320). These participants were not included in the actual study. According to the Pearson Chi-squared likelihood ratio tests, the accuracy rates did not change from the first block to the last during piloting, which indicated that feedback did not result in learning effects (accuracy per block from 1 to 4: 82.8%, 78.2%, 85.7%, 83.5%; $\chi(3)$ = 5.043, p = 0.169). This pilot helped to ensure the neutrality of the baseline part of the stimuli, as well as confirming the absence of a learning effect.

Procedure

Participants were seated comfortably in front of a computer in a well-lit room. Before the experiment, the participants completed the practice phase and became familiar with the task (6 trials: 3 IN, 3 OUT). The movie stimulus was classified as IN when the ball went in the basket, and OUT when it failed. A total of 208 trials were delivered in four sessions with three breaks each lasting 35–40 min. Each session included 52 movie stimuli comprising 26 free throws repeated twice. The movie stimuli had a proportion of 30% "IN" and 70% "OUT", to obtain the maximum amount of trials where there was an error in prediction. The stimuli included two players; however, five of the elite players recognized and reacted to one of the players of the movie, and we were forced to discard the data obtained from that stimulus. Data from 104 movie stimuli were considered during the analysis. Participants were required to predict whether the ball was going to be "IN" or "OUT", which they expressed by pressing the left or right arrow buttons for "IN" and "OUT", respectively. On average, each trial lasted 8 s. Each movie stimulus started with the wheelchair basketball player holding the ball for 1895 ms on average (SD = 63.2). One session was approximately 10 min, and the full task duration was approximately 40 min.

Participants were instructed to keep their muscles relaxed as they watched the movies. They started the task by pressing the space bar. Each trial began with a fixation cross placed on the location where the player would then appear, and participants were instructed to fix their gaze on this cross, and the player's body, throughout the trial. The movie stimuli were delivered in a pseudo-random order (i.e., more than two clips belonging to the same condition (IN/OUT) were not presented consecutively). After each movie clip, there was a black screen (range 500–1500 ms), followed by the response screen (please see Fig. 1a for the trial sequence and Fig. 1b for the movie properties). After their response, the participants rated how confident they were with their response in a visual analog scale (VAS) from "not confident at all" to "very confident". Each trial ended with the

feedback (correct or incorrect). Figure 1 describes the timeline of one trial.

EEG recording

The triggers containing timing information for EEG recordings were sent via a photodiode, a device that delivers triggers activated by a white patch placed on the bottom right corner of each movie at the last frame. Time zero was fixed at the end of the movies, since it was the same movement within each movie, presenting a mutual event in time. EEG signals were recorded by using a Neuroscan SynAmpsRT amplifier system (Compumedics, ltd) with a 60-electrode elastic headband (Electro-Cap, International, Eaton, OH) positioned according to the international 10–10 system. The signals were acquired from the channels: Fp1, Fpz, Fp2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, PO1, POz, PO2, PO4, PO8, O1, Oz, O2. The ground electrode was positioned on the scalp for ALF derivation, while the reference electrodes were applied to the left (digital reference) and right (physical reference) earlobes. A horizontal electro-oculogram (HEOG) was recorded bilaterally, and a vertical (VOEG) was recorded with electrodes positioned under the left eye. The signal was recorded with an online low-band filter 0.01–200 Hz and digitized at a sampling rate of 1000 Hz. Impedances were maintained under 5 KΩ by applying gel (ElectroGel) to all electrodes. After the data collection, the raw files were down-sampled to the rate of 500 Hz. Independent components were calculated for each participant using continuous EEG data to identify and remove eye movement and muscular artifacts (ICA; Jung et al. 2000). A mean of 3.6 components (range 1:6) were removed, using the MATLAB toolbox EEGLab (Delorme and Makeig 2004).

Behavioral analyses

Statistical analyses for the behavioral data were performed with SPSS (IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.). The mean accuracy rates were calculated for each group. We ran a mixed ANOVA design with condition and group as the within and between groups factors, respectively. The accuracy of the data guided our trial selection in our EEG analysis (See Fig. 2 for the error frequencies of each group). Trials that were not correctly identified as "IN" or "OUT" by the participant were removed. A mean of 86.3% of the trials was kept for the EEG analysis.

We also determined that the accuracy rates were free from perceptual bias: to assess whether the participants

might have a bias toward giving the "IN" or "OUT" responses more often, we ran a signal detection analysis (McFall and Treat 1999). We also controlled for the learning effect and measured the accuracy rates throughout each block of trials we determined that performance did not improve with time.

We ran a Spearman's rank-order correlation to determine the relationship between the confidence ratings and accuracy of each group.

ERP analysis

Preprocessing of the EEG data in the time domain was performed using the Brain Vision Analyzer 1.05 software (Brain-Products, GmbH). The data were band-pass filtered to 0.5–30 Hz. Epochs were time locked to the end of the players' movements, meaning that the signal was epoched in wide windows of 2200 ms, from − 1500 to + 700 ms relative to stimulus offset and were baseline corrected with a chosen interval of 200 ms during the baseline period of the movie stimulus, when the player in the video sat still (from − 1400 to − 1200 ms relative to stimulus offset). Only correctly predicted trials were included in the analysis. Each epoch was visually inspected for artifacts and residual epochs with eye blinks or epochs exceeding − 100/+ 100 µV amplitude were manually removed. Overall, 86.7% of the correctly classified trials were analyzed (~ 2560 trials in total). Bad channels were interpolated only when necessary (Perrin et al. 1989). ERPs were calculated with the *erpR* package (Arcara and Petrova 2014) in *R* Studio (R Core Team 2014).

In line with previous literature, we focused our analyses on the parietal area (Amoruso et al. 2013; Jin et al. 2011; Proverbio and Riva 2009) and mainly on the electrode Pz. We chose the window for analysis according to the part of the movie stimulus that carried the most information about the fate of the throws occurring in the last 100 ms of each movie, where the player bends his wrist and lets the ball go. Our focus on this window stems from research on how visuo-motor expertise provides advantage in reading kinematic cues (Ridderinkhof and Brass 2015; Savelsbergh et al. 2002), and that the release of the basketball is informative for experts and not novices (Abreu et al. 2012).

We used a 2 × 2 factorial design to analyze EEG amplitude over Pz with (1) condition: "IN" and "OUT", and (2) group: "players", "controls" as factors. ANOVA was conducted with the *ez* package (*ez: Easy analysis and visualization of factorial experiments,* version 4.2–2; Lawrence 2013). We also ran a Spearman correlation analysis only on the player group's amplitudes for both "IN" and "OUT" conditions with their years of expertise.

Results

Behavioral results

Figure 2 shows the mean accuracy rates for each group and each condition. The mean accuracy of the "IN" movies was 88.25% for the players and 80.76% for the controls (SD = .09, .10; respectively). In the "OUT" movies, the players were accurate in 92% of the trials and controls were 85.59% accurate (SD = .09, .12; respectively). There was a significant main effect of group on accuracy rates $F_{(1,31)} = 5.61$ $p = 0.024$, with no surviving effects on the post hoc tests.

No significant main effect of the condition ("IN" or "OUT"), or a significant interaction between the condition and group ($p = 0.153$ and .479; respectively) was found.

According to the *t* tests that were run on signal detection analysis values, the overall perceptual sensitivity of the players was significantly higher than that of the controls, $t(31) = 2.866$, $p = 0.007$ ($d'_{Players} = 2.95$, SE = .25; $d'_{Controls} = 2.09$, SE = 0.17). Analysis of the C values for bias showed that neither group had any bias toward either the "IN" or "OUT" responses, due to the stimulus frequency, $t(31) = -0.04$, $p = .970$.

There was a positive and statistically significant correlation between the VAS scores and accuracy rates, in players ($r_s (16) = 0.630$, $p = 0.009$) and controls ($r_s (17) = 0.554$, $p = 0.021$). The players had VAS scores of 69.40% (SD = 10.33), whereas controls had 60.76% (SD = 13.57).

ERP results

A repeated measures ANOVA on the ERP waveform from electrode Pz, with the factors group (players, controls) and condition ("IN", "OUT"), revealed a significant main effect of group on the mean amplitude of the signal $F_{(1,31)} = 6.17$, $p = 0.019$ during the last 100 ms of the movie stimuli (which carried the crucial kinematic information
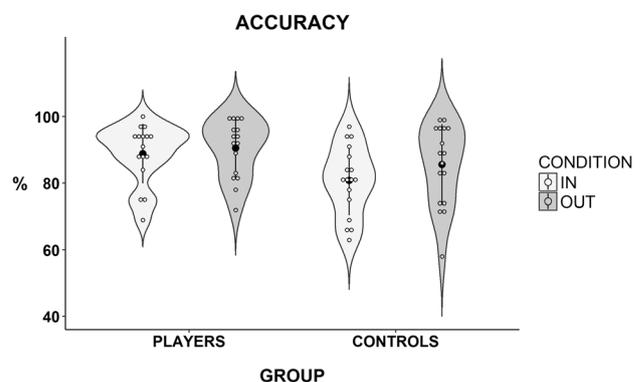

Fig. 2 Accuracy rates of each group in each condition. Players were significantly better than controls ($p < 0.001$), but no other main effect or interaction was observed. Individual dots represent the score for each subject
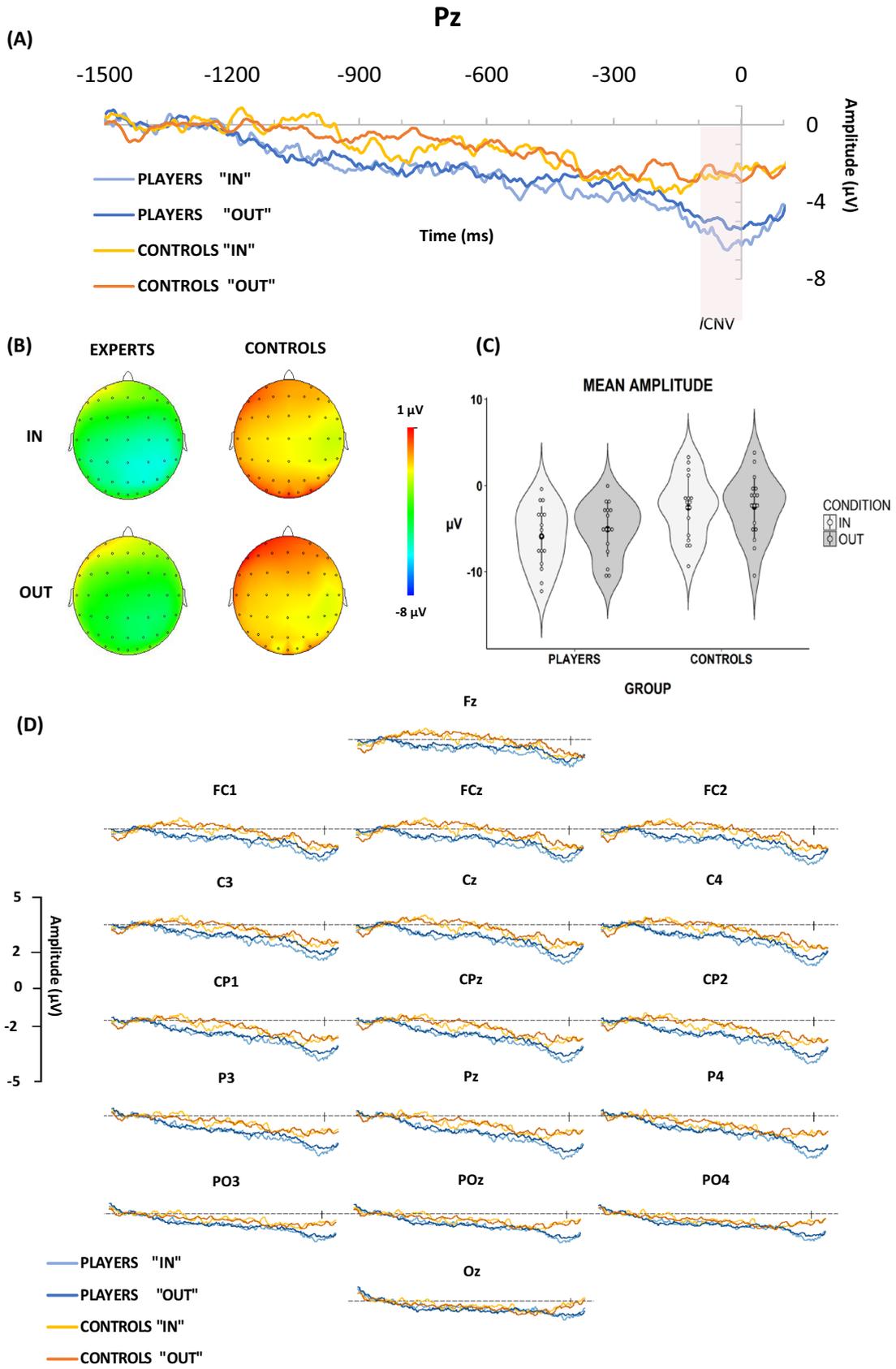
Pz

(A)

(B)

EXPERTS　　CONTROLS

IN

OUT

(C)

(D)

Fz

FC1　FCz　FC2

C3　Cz　C4

CP1　CPz　CP2

P3　Pz　P4

PO3　POz　PO4

Oz

PLAYERS "IN"
PLAYERS "OUT"
CONTROLS "IN"
CONTROLS "OUT"

◄**Fig. 3 a** ERP waveform between players and controls—the area marked in red specifies the 100 ms time window in our analysis. The waveform starts from −1500 ms before the end of the video and stops 100 ms afterward. **b** Topographic view. **c** The mean amplitudes of each group in each condition (**d**) ERP waveforms recorded in the electrodes, Fz, FC1, FCz, FC2, C3, Cz, C4, CP1, CPz, CP2, P3, Pz, P4, PO3, POz, PO4, Oz

about the basketball throw). The main effect of condition ($F(1,31) = 3.58$, $p = 0.069$) and interaction of group X condition ($F(1,31) = 2.28$, $p = 0.141$) did not reach significance. FDR corrected post hoc tests showed that players were significantly more negative in amplitude than the controls in the "IN" movies (Mean$_{Difference} = -3.35$, $p = 0.035$), but not in the "OUT" movies (Mean$_{Difference} = -2.62$, $p = 0.056$). Figure 3b shows the topography of the average signal (-100 ms–0); Fig. 3d shows the scalp distribution of the ERP waveforms from the electrodes around the midline. In neither the "IN" nor the "OUT" conditions were amplitudes significantly correlated with expertise ($r_{IN} = -0.366$, $p_{IN} = 0.082$; $r_{OUT} = -0.246$, $p_{OUT} = 0.179$).

Discussion

Experts differ from amateurs since they rely on more refined sources of information when it comes to navigating within their domain of expertise (Aglioti et al. 2008; Abreu et al. 2012). Consequently, they are better able to predict and adapt to sudden changes. In the present study, we aimed at identifying ERPs during action observation in an expert population. To do this, we tested elite athletes from the Santa Lucia Wheelchair Basketball team (players) and walking novice controls. All subjects were asked to predict the outcome of free throws presented in movie stimuli. This task allowed us to examine the neural activity with respect to domain-specific actions, as well as to record behavioral responses. Indeed, our data shows a different neurophysiological pattern for Expert athletes in comparison to controls.

Accuracy rates

As expected, the players (with a mean of 9 years of expertise) were significantly more accurate than the controls. It should be noted that the success rate across both groups of participants is 86.3%, suggesting that the shot outcome was relatively easy to predict, as was the aim of the task. However, expertise did play a significant role in the accuracy of the prediction of the fate of the basketball shots.

ERP signals

Our main hypothesis was that the neurophysiological correlates of action observation are modulated in expert players.

Our analysis shows that the players had a significantly larger parietal EEG negative amplitude compared to controls during the key point of the observed throw: when the wrist closed to complete the shot. This may be reminiscent of the results that expert basketball players focused on the kinematics of the shot while the expert watchers (i.e., non-players) used later cues like the ball trajectory in order to reach successful predictions (Aglioti et al. 2008). Upon visual inspection of the topography and the scalp distribution of the waveform (Fig. 3d) we have found similarities with the analyzed waveform and the oCNV.

Action effect prediction has been associated with a negative deflection over the parietal electrodes (Hughes and Waszak 2011; Jin et al. 2011; Savoie et al. 2018). Our task had some similarities and some differences with respect to the traditional set up that elicits a CNV. In our task, the cue (the beginning of each clip) was uninformative as to the required response and it only indicated that there was going to be a response in roughly 1.5 s. Then the actual information regarding the response was carried within the last ~100 ms of each clip. Nevertheless, the slow negative waveform is present for both groups. The oCNV amplitude in experts is significantly more negative compared to the controls. This result aligns well with the idea that a CNV is elicited not only during the observation of a partner's action (Kourtis et al 2010; 2013), but also during the observation of an expert's domain of expertise (Wang and Tu 2017). Wang and Tu (2017) found that CNV was smaller in badminton players compared to controls when predicting the height of badminton shots with a high uncertainty. Increased oCNV amplitudes in controls has been interpreted as a greater need for attentional control. While this finding seems in contradiction with our results, in our task we aimed to have a ceiling effect, which meant that for the players, there was little uncertainty. The parietal negativity we report has similarities with CNV, in terms of its occurrence during action prediction and latency. Contrary to our prediction, our results did not show a difference in the ERP waveform regarding "IN" and "OUT" shots within groups, however, there was a main effect of group in the amplitudes, which survived the post-hoc tests for the "IN" condition. In other words, the players had greater negative parietal activity compared to the controls in the "IN" condition. We speculate that the difference revealed in the late oCNV might be due to the observed domain-specific activity (i.e., observational *l*CNV). We suggest that this negative amplitude is associated with higher activity in sensorimotor areas associated with expertise during the observation of a domain-of-expertise action (Hughes and Waszak 2011; Jin et al. 2011; Savoie et al. 2018), but further investigation is required to validate this claim. The correlation analysis regarding expertise and ERP amplitude was not significant for either "IN" or "OUT" conditions. This is likely due to the small sample size, as differences in

amplitude are very small and would require a greater sample of experts.

By occluding the ball trajectory, the present study builds on Agliotti and collaborators' previous findings (Agliotti et al. 2008) and highlights the EEG correlates associated with action outcome prediction based on movement kinematics (i.e., arm and wrist movements). When compared to the controls, the players show significantly more negative deflection in parietal regions during the observation of the kinematics of a basketball shot for the "IN" condition, but the significance does not survive the post hoc tests in the 'OUT' shots. The significant difference between these two groups in the "IN" shots may stem from the uncertainty that exists for non-players, especially in the 'IN' shots. Once the decision for the 'OUT' shot has been made, the observer will no longer have any uncertainty, whereas for the 'IN' shots, even for mere milliseconds, there may be more attention necessary until later in the movie. Thus, a scenario where players—who do not seem to experience uncertainty in either condition—compared to controls have a more negative ERP signal regarding the 'IN' shots can be tentatively interpreted as occurring due to the continued uncertainty which the controls might experience. We did not observe any clear peak that could be considered an error-specific component such as a frontal observed error-related negativity (oERN) for the "OUT" shots (where an error in kinematics occurs for the shot to fail). This may stem from the overlap of other components such as error positivity (Pe) over ERN, dependent on specific task features (e.g., Panasiti et al. 2016). It may also be due to the continuous nature of our task, making a clear event-related potential difficult to extract. Furthermore, the timing of the movements building up to the shot varied across our movie stimulus.

It has been shown that visual and motor training have different implications in action observation (Casile and Giese 2006; Inuggi et al. 2018). Similar to our results, it was recently shown that subtle intention-specific kinematic information can be decoded from a network that involves parietal regions (Koul et al. 2018). In our stimuli, the intention remains to successfully shoot the basketball through the hoop, but when the execution of the movement is erroneous, this information is also carried within the movement kinematics. Crucially, during observation of the moving body, the parietal region of expert dancers was shown to contribute to integrating kinesthetic perception with the representation of the dance syntax (Bachrach et al. 2016). In our study, we focused our analyses on the electrode level, which prevents direct comparison to neuroimaging studies that specify the parietal region in the context of expertise. Nevertheless, our results are in line with those of other studies that have shown different brain activation for experts with various imaging techniques and tasks. In this study, we have shown a parietal negativity during the crucial moments of action cues

for anticipation during a basketball shot. Successful action integration and prediction allows expert players to more rapidly and more effectively adjust in situations that require their expertise (Hack et al. 2009; Wu et al. 2013). Experts are therefore better in action execution during unexpected situations that may arise in the domain of their expertise and show different AON activation during action perception tasks (Wang and Tu 2017; Wang et al. 2017). However, in studies that use tasks such as the Flanker task (not directly relevant to the particular domain of expertise), the neurophysiological signals from expert athletes do not always display differentiating patterns compared to non-athletes, even in the presence of better reaction times or performance (Di Russo et al. 2010; Wang et al. 2017). Moreover, the type of expertise (e.g., in the kind of sport that is the focus of a study) drives which cognitive skills are enhanced, such as cognitive control or spatial abilities (Chan et al. 2011; Yamashiro et al. 2015), and a better understanding of these measures might lead to better skill-specific training. Previously, Amoruso et al. (2014) demonstrated, in expert tango dancers, that anticipatory neural activity regarding movement recognition differed between groups of experts and novices, and that semantic neural responses such as N400 predicted motor expertise. In our study, we investigated how the level of expertise might impact a specific domain of action observation.

During the execution of a basketball free throw, the players use both visual and proprioceptive cues. Maglott et al. (2019) tested basketball players from a university team (experts) and recreational basketball players (non-experts) and asked them to predict the fate of their own shots (verbally indicating "in" or "out") without seeing the actual outcome. The results showed that university team players—compared to recreational ones—were more accurate in predicting their own correct throws, but worse in predicting their missed shots (i.e., worse than chance level). In Maglott et al. (2019), further analyses showed that experts had a bias in perceiving their own shots as "IN". While this result may seem at odds from our current results, the different patterns may stem from the difference in the methods used, such as the first versus third person perspective, or execution versus observation. In our task we aimed to have a ceiling effect to ensure a maximum number of trials in which the action outcome was correctly predicted in each group, and for the EEG analysis, only the correctly predicted trials were considered.

Anticipation or outcome prediction can be manipulated statistically, by expectations that are set within specific task requirements or by the need to rely on the movement of others (Heil et al. 2018; Pezzetta et al. 2018). However, different neural signatures can be observed with anticipation in statistically unpredictable situations. Furthermore, action anticipation based on biological kinematics can have an impact on neural activation. Experts are able to simulate the observed

domain-specific action (Senna et al. 2014; Tomasino et al. 2012). While the heterogeneity of the athletes' physical ability impedes addressing straightforward questions regarding the effects of actual physical ability/disability on the AON network, it still provides a setting in which physical expertise can be studied. Wheelchair basketball requires skills acquired with more difficulty than regular basketball, and perceptual-motor training (obtained by a visual constraint that forced participants to use target information as late as possible) has a positive impact on future successful shooting percentages (Oudejans et al. 2012). There is a lot of interest in how expertise affects not just the behavior but also plasticity in the brain, and research in this area has had a valuable impact on the understanding of the mechanisms underlying learning, skill acquisition, and the rewiring of the brain after an acquired motor disability.

Future directions and conclusions

The relationship between expertise and AON engagement has been modeled within different frameworks. Recently, a quadratic relationship between increasing familiarity and the accuracy of predictions was proposed (Gardner et al. 2017). Gardner and colleagues trained participants in guitar movements. They demonstrated that BOLD activity in the AON is present during both highly familiar and highly unfamiliar observed actions, either due to more accurate predictions in the former, or due to continuous updating in the latter. It may be beneficial for future EEG/MEG studies to examine how parietal negativity during domain-specific action observation due to sports expertise might be affected with a manipulation that could result in a quadratic relationship. In our study, we compared subjects that were expert players and completely naïve controls. We aimed to describe expertise-related observational properties, but we did not induce expertise acquisition (e.g., through learning) within our paradigm. It is necessary for future studies to assess how motor skill learning occurs, or more specifically how motor expertise acquisition induces changes in the brain (Ossmy and Mukamel 2018), to have online information about training-induced brain plasticity. Future research would benefit from using immersive virtual-reality environments to provide more controlled setups (Ozkan and Pezzetta 2017; Pavone et al. 2016; Spinelli et al. 2018; Pezzetta et al. 2018), targeting specific features of action observation in expert groups with certain physical abilities, with the aim of making effective comparisons.

Overall, we report ERP signals evoked by action observation in wheelchair basketball expertise. While we acknowledge that the sample of athletes in this study is comparatively small, our data supports and extends the literature by demonstrating more negative activity in elite athletes, especially when the expert players focus on crucial information.

Crucially, our data also further support the relation between motor experience and anticipation expertise via embodiment mechanisms and raises new questions regarding the acquisition of motor skills after injury and the different levels of expertise.

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