Brain Dynamics of Visual Anticipation During Spatial Occlusion Tasks in Expert Tennis Players

Anticipation of others' actions is a major area of investigation in sport since its beginning in the 1970s (Loffing & Cañal-Bruland, 2017). Visual perception plays an important role in action anticipation, especially in team ball games, combat sports, and racket sports (Brenton & Müller, 2018; van der Kamp et al., 2008), in which the ability to quickly and accurately pick up relevant information reduces the time of decision-making and, thus, speeds up the response (Savelsbergh et al., 2005; Shim et al., 2006). In recent interpretations, anticipation is mainly determined by the effectiveness of maintaining selective attention towards task-relevant stimuli, such as postural and kinematic cues of the opponent's movements (Müller & Abernethy, 2012). Within this framework, visual anticipation is "the ability to perspective information scaled in units of maximum action capabilities" (Montagne et al., 2008). This view has been integrated into affordance-based models of perceptually guided action (Montagne et al., 2008), so that a fine-tuned motor resonance system, resulting from extensive motor practice, is needed to improve sensorimotor performance and achieve better action anticipation (Aglioti et al., 2008).

Elite athletes develop sport-specific cognitive skills and exhibit superior integration across the domains of perception, cognition, and action (Yarrow et al., 2009). Different studies demonstrated that, compared to novices, expert athletes achieved better performance, since they were able to more effectively integrate kinematics information to predict the action outcome of their opponents (Güldenpenning et al., 2013; Huys et al., 2009; Jin et al., 2011; Müller & Abernethy, 2012; Piras et al., 2014; Smeeton & Huys, 2011; Smith, 2016; Williams & Jackson, 2019). According to the 'common coding' hypothesis (Prinz, 1997), which describes the functional relationship between perception and action, skilled players in racket sports seem to process kinematic information in a manner that reflects the sequential recruitment of movement segments, by integrating cues,

provided by an opponent's more proximal regions (e.g., shoulder, hips) in planning an action to initiate an appropriate movement response (see (Abernethy et al., 2008)).

Spatial occlusion is the commonly used approach to investigate if and which postural and kinematics information coming from specific body areas would help predicting action-outcome of opposing players (Cañal-Bruland et al., 2011; Jackson & Mogan, 2007). With this approach, the observed action is manipulated by deleting different body areas of the opponent (Williams & Jackson, 2019), and any performance decrement in the occluded condition, with respect to a non-occluded control condition, would suggest that the information coming from the missing element might play a crucial role in anticipation, either on its own or in conjunction with other cues (Causer et al., 2017; Smeeton & Huys, 2011).

However, this approach ignores the intrinsic nature of temporally extended process of decision making in sport, which requires a dynamic perspective considering perception, cognition, and action. Electroencephalography (EEG) has excellent high temporal resolution, making it ideal for tracking the rapid execution of sensory, cognitive, and motor processing during anticipation. Few studies have investigated the Event Related Potential (ERP) components during an anticipation task in racket sports. In these studies, players with different expertise were asked to observe video clips of opponents and predict ball kinematics and landing position as fast and accurately as possible. More experienced players made significantly faster and more accurate judgments than less experienced players or novices. Consistently, they showed enhanced amplitudes of the occipital P2 and the central-parietal P3 components (Jin et al., 2011; Shangguan & Che, 2018). The amplitude of the occipital P2 component has been associated with a quick detection of the stimulus salience and cognitive matching between sensory inputs and stored memory (Carretié et al., 2001; Gontier et al., 2008; Thorpe et al., 1996). The larger P3 in more experienced athletes has been associated with higher amendment of context updating and improved memory recognition (Hammond et al., 1987; Liu et al., 2017; Polich & Lardon, 1997; Shangguan & Che, 2018). Accordingly, a larger P3

component was also found in a group of trained participants who attended a 12-week badminton training course, with respect to non-trained controls (Liu et al., 2017). Some of these studies investigated ERP components time-locked to the onset of a video clip (Jin et al., 2011; S. Liu et al., 2017; Shangguan & Che, 2018), which was usually triggered by the sudden appearance or changing of an athlete posture from a baseline background. However, the subsequent key events in the video (i.e., the body and racquet movements until the ball-racquet contact) occur in an ambiguous time relationship with respect to the stimulus onset. The ERPs need precisely timed event, so that the brain activity is time-locked with the stimulus. Other studies used stationary abstract patterns as stimuli, i.e., a stimulus without specific relationships to anticipation skill in sport, arguing that ERP components are measuring generic cognitive processes in different groups of athletes (Lucia et al., 2022; Nakamoto & Mori, 2012). These processes are not sport-related processes. Finally, other racquet-sport studies used event-related but not phase-locked analysis, as time-frequency analysis (Denis et al., 2017). To provide an unambiguous time-reference for ERP recording, in our study we chose to use stationary stimuli, i.e., single-frame pictures of players at the time of ball-racquet contact, providing, based on previous studies (Cañal-Bruland et al., 2011b), a reliable basis for accurate judgements of outcome.

To the best of our knowledge, so far, no studies have investigated the neural correlates of visual anticipation by manipulating with stationary stimuli (i.e., single frame picture) the postural information related to the body of opponents by means of spatial occlusion protocols. In the present study, we investigated brain responses related to anticipation during a spatial occlusion protocol in two groups of professional tennis players with different levels of expertise. We hypothesized that the lack of postural information due to the occlusion of salient body areas of the opponent would affect the brain processing related to stimuli and would be also associated with a reduced performance. With respect to previous studies based on video presentation, showing that kinematics (i.e., the analysis of movement) is the overriding factor, we expect that expert players would show a

better performance with respect to less skilled players, also when stimulus cues are limited, as in a single-frame stimulation.

To this aim, we investigated the prediction of action-outcome, in terms of accuracy and response time, and the amplitude of the post-stimulus ERP components associated with the specific body occlusion conditions. Current source density analysis, performed by the "exact low resolution brain electromagnetic tomography" (eLORETA, Pascual-Marqui, 2002), was used to identify the sources of the observed components. Previous relevant ERP studies, including source localization analyses, were used to guide the interpretation of our findings. More specifically, we have investigated the effect of spatial occlusion on the components related to early sensory and perceptual processes (the P1 and the N1, e.g., Di Russo et al., 2019), decisional processes (the anterior P2: e.g., T. Liu & Pleskac, 2011; Potts, 2004a; elsewhere called prefrontal P2, pP2: e.g., Perri et al., 2015), and higher cognitive processes (the P3). We also described the effects of spatial occlusion and player expertise on the recently discovered prefrontal components involved in perceptual and visuo-motor awareness (the pN1, Pp1, and the pN2, e.g. Di Russo et al., 2016, 2019), originating in bilateral anterior insular cortices.

It is known that three-dimensional visual depth modulates the first ERP visual components (Liu & Pleskac, 2011) and a disparity between ERPs elicited by 2D or 3D scenes has been described (Duan et al., 2018), so that scenes with more homogeneous depth maps tended to elicit larger disparity-specific responses. Thus, in studying brain responses to visual stimulations in which the depth is an important element to retrieve kinematic information, the stimulus presentation modality (2D or 3D) should be addressed. Moreover, a recent meta-analysis revealed that the in-situ condition consistently showed an advantage of expert players over novices (Travassos et al., 2013). Therefore, to investigate performance and person-task-environment interaction in a multimodal and multidimensional perspective, we should move toward more ecological protocols (Bertollo et al., 2020). A first step in this direction is to create more realistic and specific stimuli with stereoscopic

vision and more ecological environment. Thus, a further aim of this study was to understand if the stimulus presentation modality (i.e., 2D or 3D) would modulate both performance and brain processing related to specific spatial occlusion conditions. For instance, literature has reported contradictory results on tennis players performance in comparing 2D and 3D stimuli, probably due to the different technology used to achieve 3D vision. While 3D stimuli might induce faster responses as well as higher accuracy with respect to 2D stimuli by recreating real sport situations, thus providing salient motion-in-depth information to the participant (Bideau et al., 2010; Craig, 2013; Katz et al., 2006), no performance improvement in intercepting an opponent tennis serve direction under weak and strong 3D conditions has also been reported (S. Liu et al., 2017).

Methods

Participants

To determine the minimum sample size, a priori analysis for a mixed analysis of variance (ANOVA) design (G*Power 3.1.9.2) was performed. No previous ERP studies are available reporting the effect size of the interaction between the conditions used in our study. Thus, a priori values for the electrophysiological variables were estimated (Guo et al., 2013). We used the automatic direct method available in G*Power, with a medium effect size of 0.25, α error probability = .05, power (1- β error probability) = .95, number of groups = 2 (EP and LEP); number of measurements = 5 (spatial occlusions) and ϵ = 1. A minimum number of 32 participants was required to have an actual power of .96.

Thirty-seven professional male tennis players (23.4±5.5 years old) were enrolled in the study. Expertise level was ranked according to the criteria of the Italian Tennis Federation for male players (http://cmscomitati.federtennis.it/PDF/MetodoClassificheFederali2020.pdf) that ranked from 4.6 (minimum expertise) to 1 (maximum expertise). Ranking below 2.2 identify professional

athletes playing at international and national level. Participants were classified into two groups, based on their expertise, following the model proposed by (Swann et al., 2015). One group was defined Expert Players (EP, corresponding to clusters 2, 3,4 in Swann et al., 2015) and was composed by 18 athletes (mean age 24±6 years) with expertise level corresponding to a rank<2.7 (median 2.4), a mean of 16±5 years of tennis-playing experience and an average of 266±113 tournament matches. The other group was composed by 19 Less Expert Players (LEP, cluster 1 in Swann et al., 2015, mean age 23±5 years) with expertise level ≥2.7 (median 3.2), a mean of 12±4 years of tennis-playing experience and an average of 101±50 tournament matches. LEPs had 4 years less tennis-playing experience and under half of tournament matches than EPs. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-normal vision, and reported no history of neurological or psychiatric disorders or brain injuries. The study was approved by the local Ethical Committee and all subjects signed a written informed consent.

Stimuli and task design

Each participant was tested in a sound-attenuated dimly lit room after applying the EEG electrodes. They comfortably seated in front of a 24" LCD monitor at a distance of 114 cm. The sitting position was adjusted to keep the eyes at the monitor level, so that the stimulus presentation was in the fovea. To limit movement artifacts, participants were required to remain as still as possible during data collection, avoiding head movements and eye blinks, especially during stimuli presentation. During the whole experiment, participants did not receive any feedback about response accuracy and response time of their performance.

The experimental task aimed at examining the participants' ability to predict the ball landing position by viewing images that were spatially occluded by erasing different parts (Jackson & Mogan, 2007). To this aim, we used images of opponent players hitting the tennis ball with

different action intentions under 4 spatial occlusion experimental conditions: legs occlusion, trunk occlusion, racket and arm occlusion, ball occlusion (Figure 1A). Full body image (no occlusion) was used as control condition. The height and width of the opponent players was 3.2 cm and 2 cm, corresponding to a vertical visual angle of 1.3° and a horizontal visual angle of 1°. The images were extracted as single video frames (see "Image stimuli editing" section).

The action intention options, which were equally balanced across all conditions, were represented by left/right directions and long/short balls, as well as backhand and forehand shots. The image stimuli were presented in both classic 2D mode and 3D mode. The 3D stereoscopic view was achieved by using red-cyan anaglyph glasses. A full description of the technical details concerning video-frames preparation and handling is provided in the supplementary materials.

Participants underwent 400 experimental trials (80 trials for each spatial occlusion) for each presentation mode (2D or 3D). Given the left/right, long/short and backhand/forehand shots, for each spatial occlusion there were $80/(2 \times 2 \times 2) = 10$ trials repetition per shot type.

Each trial (Figure 1B) started with a baseline condition showing the static image of a player in an attending position for 4 s. Afterwards, the baseline image was replaced by an image displaying the player hitting the ball with one of the different spatial occlusions according to the experimental conditions (i.e., legs occlusion, trunk occlusion, racket and arm occlusion, ball occlusion, no occlusion). Participants were asked to carefully look at image stimuli and to judge as quickly and accurately as possible the ball landing position. The images with the different spatial occlusions were displayed until the participants made a response or for a maximum of 1.5 s. Participants positioned their right hand palm down on a numeric keypad and their right index finger on the number 5; they were asked to press the numbers 1, 3, 4 and 6 to indicate in which of the four court zones the ball will come in, i.e. beyond the half court in the left and right part (1 and 3, respectively); within the half court in the left and right part (4 and 6, respectively). The screen

turned black immediately after the response. The inter-trial stimulus was set to 1 second, in which the screen remained black.

For each presentation mode (2D and 3D), the 400 experimental trials were split into 5 blocks of randomized 80 trials each, with a break between blocks. Each block lasted approximately 8-9 minutes. Before beginning each experimental phase, participants performed a learning session of 26 trials for each presentation mode (2D and 3D) to familiarize with the task, using different pictures from those included in the experiment. Since the entire protocol lasted approximately 2 hours the two presentation modes were performed by participants in consecutive days to prevent fatigue. The 2D/3D conditions were counterbalanced across participants.

INSERT FIGURE 1 HERE

Image stimuli editing

The image stimuli used for experiments were single frames extracted from videos. Video were obtained by means of a parallel mount upon a "Cartoni" fluid tripod with n°2 Canon C300 camera kit with n°2 Canon Zoom Lenses 16-35 mm 2.8. The cameras were screwed on a 250 mm iron plate, with a distance of 10 mm between the 2 bodies of the cameras (counting from the center of the cameras' sensor). We got the tripod on the medium point of the end line of the tennis field at a height of 150 cm from the ground to the center of the camera sensor. The decision to record the stimuli from this perspective was based on the rationale that this is the same visual perspective adopted by tennis players during the practice and the match. This "first person" viewing perspective ensured ecological validity (i.e., a good match between the training session and competition where similar visual scenes are encountered). The two cameras were set with the following parameters: focal 24mm, 4 aperture, 400 ISO, 1/50 shutter, recording in 1920x1080 squared pixels ratio, in 25 frame per seconds progressive, in 10 bits colored.

Four right-handed players featured in the video. For the recording, one of the players stood positioned on the back line of the court and balls were sent toward the players by a ball machine positioned centrally on the baseline in the opposing half, out of the sight of the camera. The position of the camera allowed to have the point of view of the opponent player positioned on the baseline. The player being filmed performed both forehand and background strokes moving just one meter to the right and to the left from the center line, this to avoid any influence of contextual information. The players were instructed to perform shots clearly aimed to the left or right, short and long hand side of the court, to have the cleanest shots possible, without forms of disguising. Each clip was judged as to the final position of the ball and 50 shots for each player were recorded. Shots hitting the net were removed, as well as shots where the ball landed in the "tramlines" or those which had been noted as "doubts" by an observer during filming. Finally, we selected the shots of just two athletes as stimuli for the task. The other players' shots were used for the practice trials. This allowed us to reduce the possibility that using only one performer stimuli could create idiosyncrasies, which may make it easier or harder to predict event outcome.

We used the Adobe Suite CC (latest version 2016/17), and Photoshop CC were used for the post-production and editing, and Premiere Pro CC with the Stereoscopic 3D alpha Chanel system (in RGB color space) for 3D video editing.

Behavioural data

Individual performance was evaluated in terms of the mean percentage of correct answers (accuracy) and the mean response time (RT). Response was considered correct based on the side of ball landing position (right or left). RTs were defined as the time between the start of the stimulus (picture with occlusion) and the button press. According to Filipcic et al. (2020), response times slower than 1.5 s were considered as wrong responses. Since accuracy values deviate from normality in some occlusions (as assessed by Kolmogorov-Smirnov test), we applied an arcsin

transformation (http://www.biostathandbook.com/transformation.html). We applied a 2x5x2 mixed-factor design analysis of variance (ANOVA) separately on accuracy and RTs, with *Group* (EP vs. LEP) serving as between subject factor and *Occlusion* (no legs, no ball, no racket and arm, no trunk, no occlusion) and *Mode* (2D vs. 3D) as within-subject factors. Greenhouse-Geisser correction was applied when the assumption of sphericity was violated and partial eta-squared (η_P^2) was used as a measure of effect size. Post-hoc comparisons were performed by paired t-tests (Bonferroni corrected) whenever the main effect for *Occlusion* in ANOVA design resulted significant. Since a non-linear transformation was applied to accuracy values, once done the statistical test, the inverse transformation was applied to mean and lower/upper confidence interval limit to obtain accuracy in the original measure unit (percentage of correct answers).

EEG recording and analysis

EEG data were recorded by means of a 128-electrode net (version 1.1, Electrical Geodesic), placed according to an augmented 5–5 international system. The skin/electrode impedance was measured before recording and kept below 5 k Ω . EEG data were sampled at 250 Hz and stored for processing offline.

Data were filtered between 0.1 and 40 Hz (forward-backward second-order Buttherworth filter). A semiautomatic Independent Component Analysis-based procedure (Barbati et al., 2004; Croce et al., 2019) was applied to identify and to remove cardiac and/or ocular artifacts, as well as activity coming from additional movements during the task and instrumental noise. Saturated or corrupted EEG intervals were rejected by visual inspection. EEG signals were transformed to the common average reference. Data were segmented in epochs from -200 ms before to 1.5 s after the stimulus onset. A mean of 40 cleaned trials (mean: 40, standard deviation: 6, range: 31 – 50) were averaged for each condition. The baseline was chosen in the period of 100 ms preceding the stimulus (-100/0 ms).

The selection of time windows and sites for statistical analyses was based on the topographical distribution of the ERP components assessed by visual inspection (see results section). First, the grand means of the ERP waveform, averages for each condition across all subjects, were evaluated and peaks, corresponding to ERP components, were identified. The time windows were centered on each of these peaks. The windows width was chosen to include all individual peaks of the same component while excluding peaks of different, adjacent components. No latencies differences were evidenced among peaks of different occlusions or between presentation modality (2D, 3D), nor were differences found between EP and LEP latencies. Moreover, no differences in topography across conditions were evidenced. For these reasons, for each condition and mode presentation, the following ERP components were calculated as the mean amplitude on selected electrodes and in selected time windows, as follows: the P1 on O1 and O2 sites and the pN1 on Fpz site in the 80-110 ms time window; the N1 on PO7 and PO8 sites and the pP1 on AFz site in the 110-160 ms; the Pp2 on FCz site in the 160-280 ms; the P2 on POz site in the 250-350 ms; the P3 on Pz site and the pN2 on Fpz site in the 400-500 ms. A 2x5x2 mixed-factor design analysis of variance (ANOVA) was separately applied to the pN1, pP1, P2, pP2, pN2 and P3 components, with Group (EP vs. LEP) serving as between subject factor and Occlusion (no legs, no ball, no racket and arm, no trunk, no occlusion) and Mode (2D vs. 3D) as within-subject factors. The P1 and N1 components are bilateral (evaluated on O1 and O2 sites and on PO7 and PO8 sites, respectively). For these components, to evidence possible hemispheric asymmetries, an additional within subject factor Hemisphere (left, right) was considered.

To identify the neural sources underlining significant differences between conditions, (occlusion vs no-occlusion, EP vs LEP, 2D vs 3D) we performed a current density analysis in 3D MNI space using eLORETA (Pascual-Marqui, 2002). The current source density distribution of the mean ERP of each condition was estimated in the time intervals where statistical differences were found. The electrical potential lead field was computed using the boundary element method on a

MNI template (Fuchs et al., 2001), and cortical activity power was estimated on a grid of 6239 voxels, with a spatial resolution of 5 mm. Difference between conditions was visualized on an average cortex (Van Essen, 2005).

Results

Behavioral Results

Mixed factor ANOVA on accuracy showed a significant main effect of *Occlusion* [F(4,140)=60.36, p<.001, η_P^2 =.633] and *Group* [F(1,35)=9.76, p=.004, η_P^2 =.218]. No significant effects were found for *Mode*, nor for interactions (see Supplementary Materials). Post-hoc test revealed that accuracy in trunk (mean ([95% confidence interval]: 53.6 % [52.4% – 54.8%]) and ball occlusion (62.0% [62.5% – 66.3%]) conditions was lower than in no occlusion (64.4% [60.3% – 63.7%]), (corrected p<.005, Cohen's d=2.04, and p=.017, Cohen's d=.73 , respectively; see Figure 2A). EP showed higher accuracy than LEP (64.0 % [62.2% – 65.9%] vs 59.7% [57.7% – 61.7%], Figure 2A).

Mixed factor ANOVA on RT showed a significant main effect of *Occlusion* [F(4,140)=6.02, p<.001, η_P^2 =.147]. Post-hoc tests revealed that participants were faster in no occlusion (mean [95% confidence interval]: 944 ms [906 ms – 982 ms]) than trunk (983 ms [941 ms – 1025 ms]) and ball occlusion (969 ms [928 ms – 1010 ms]) conditions (corrected p=.003, Cohen's d=1.46 and p=.016, Cohen's d=1.55, respectively, Figure 2B). Also a significant main effect of *Mode* [F(1,35)=5.20, p=.029, η_P^2 =.129] was found, with faster RTs in 2D than in 3D condition (934 ms [886 ms – 982 ms] vs 989 ms [948 ms – 1029 ms], Figure 2B). No significant effects were found for *Group*. Moreover, a significant interaction *Occlusion* × *Mode* [F(4,140)=4.22, p=.003, η_P^2 =.108] was found. Only the difference between trunk occlusion vs no occlusion was higher in 2D than in 3D condition (60 ms [32 ms – 90 ms] vs 17 ms [-4 ms – 38 ms], paired t-test 2D vs 3D: t(36)=2.89, p=.006, Cohen's d=.59). No other significant interactions were found (Supplementary Materials).

INSERT FIGURE 2 HERE

ERP results

Figure 3 shows ERP waveforms averaged across 2D and 3D modalities for each spatial occlusion and for the control condition (no occlusion) in a selection of EEG channels. The following ERP components can be disclosed: a bilateral parieto-occipital positivity (the P1 component) and a medial fronto-polar negativity (the pN1 component) in the time window between 80 ms and 110 ms; a negative component in the parieto-occipital regions (the N1 component), more pronounced in the right hemisphere, and a medial prefrontal positivity (the pP1 component) in the time window between 110 ms and 160 ms; a medial positive central-parietal activity in the time window from 160 to 280 ms (the pP2 component) a and a positive component over parieto-occipital areas (the visual P2) from 250 to 350 ms; a large negative prefrontal activity (pN2) and a large positivity over medial parietal area (the P3 component) can be seen starting from 300 ms.

INSERT FIGURE 3 HERE

ANOVA on the P1, pN1 and P2 did not show significant main effects or interactions (Supplementary Materials). The N1 showed a significant main effect of *Hemisphere* [F(1,35) = 11.54, p = .002, η_P^2 = .228], N1 amplitude being higher in the right than in the left hemisphere, and a significant *Hemisphere* × *Occlusion* interaction [F(4,140) = 3.18, p = .015, η_P^2 = .083]. Reduced models were separately applied on the right and left N1. No significant effects or interactions were found in the left hemisphere. On the contrary, the right N1 showed a significant effect of *Occlusion* [F(4,140) = 3.99, p=.004, η_P^2 = .102]. A significant effect of *Occlusion* [F(4,140) = 3.14, p = .016, η_P^2 = .082] was also found for the pP1. Post-hoc comparisons showed that both the N1 and the pP1 were lower in trunk occlusion than in no occlusion (for N1: -.1 ± .2 μ V vs -.5 ± .2 μ V, corrected p =

.009, Cohen's d = 1.82; for pP1: -.1 \pm .1 μ V vs .4 \pm .2 μ V, p=.008, Cohen's d=1.24; Figure 4 A). For the N1 and the Pp1, no significant effects were found for *Mode* and *Group*, nor for interactions (Supplementary Materials).

For the pP2, a main effect of *Occlusion* was also found [F(4,140)=5.25, p=.001, η_P^2 = .130], with a lower amplitude in trunk occlusion than in no occlusion (.4 ± .2 μ V vs .6 ± .2 μ V, p=.020, Cohen's d =0.90) and in ball occlusion than in no occlusion (.3 ± .2 μ V vs .6 ± .2 μ V, p=.010, Cohen's d =1.23; Figure 4 B). No other significant main effects or interactions were found (Supplementary Materials).

INSERT FIGURE 4 HERE

ANOVA on the pN2 showed significant main effects of *Occlusion* [F(4,140) = 6.76; p<.001, η_P^2 = .162] and *Group* [F(1,35) = 5.27; p=.028, η_P^2 = .131]. Post-hoc comparisons showed that the pN2 was higher in trunk occlusion than in no occlusion (-2.1 ± .3 μ V vs -1.3 ± .3 μ V, corrected p = .003, Cohen's d=1.06; Figure 5A) and EP showed higher amplitude than LEP (-2.1 ± .3 μ V vs -1.1 ± .3 μ V, Figure 5B). For the pN2, no main effect of *Mode* or significant interactions were found (Supplementary Materials).

ANOVA on the P3 component showed only a significant main effect of *Group* [F(1,35) = 5.73; p=.022, η_P^2 = .141]. As for the pN2, EP showed higher P3 amplitude than LEP (3.1 ± .4 μ V vs 1.7 ± .4 μ V, Figure 5B). Also, for the P3, no main effect of *Occlusion* and *Mode* or significant interactions were found (Supplementary Materials).

INSERT FIGURE 5 HERE

Results are summarized in table 1.

To identify the cortical sources underlying the differences of ERP component amplitude between conditions, eLORETA was applied to mean ERPs. Figure 6 shows the difference of ERP cortical sources between two conditions: red/yellow colours indicate stronger source strength in first labelled condition than in the second condition, cyan/blue colours indicate stronger source strength in the second condition than in condition first one.

INSERT FIGURE 6 HERE

In the time window between 110 ms and 160 ms, stronger sources in no occlusion than in trunk occlusion were present around the right extrastriate visual areas (the N1). A stronger source in no occlusion than in trunk occlusion was found also in prefrontal cortex (the pP1), within the superior and medial frontal gyri and limbic areas (Figure 6A). In the time window between 160 ms and 280 ms, stronger sources in no occlusion condition than in trunk occlusion were evidenced in frontal and limbic areas (the pP2). The same areas were found in comparing no occlusion with ball occlusion (Figure 6B). In the time interval starting from 250 ms, stronger sources in trunk occlusion than in no occlusion conditions were found in prefrontal areas and limbic areas (the pN2, Figure 6C). The comparison of EP vs LEP source strength in this time interval (Figure 6D) revealed stronger source activity in EP within precuneus, bilateral inferior parietal lobule, left middle and superior frontal gyri, and (bilateral) dorsolateral prefrontal cortex.

Discussion

In the present study, we investigated how two groups of expert tennis players (EP and LEP) anticipated the outcome of an action by means of visual information related to the opponent's body, using different spatial occlusions and stimulus presentation modes (2D, 3D). Regardless of expertise, participants were less accurate and slower when trunk and ball were occluded as

compared to the other conditions. These results are not in agreement with previous studies on tennis anticipation with spatial occlusions (Cañal-Bruland et al., 2011; Williams et al., 2009; Ward et al., 2002), which observed the greatest decrement in performance accuracy in the arm and racket condition, highlighting the importance of end-effector information when anticipating opponents' intentions (Cañal-Bruland et al., 2011; Williams et al., 2009; Ward et al., 2002). Nevertheless, this discrepancy is reconciled when considering the different stimulations and experimental set-ups among studies. First of all, we used as stimulation a single video frame sampled at the time of ballracquet contact. On the contrary, the studies of (Williams et al., 2009) and (Cañal-Bruland et al., 2011) used as stimulation video-frames of headless stick figures (obtained from 18 points). The biological motion was perceived by the movement of the sticks, the clips were occluded during the video clip or at the ball-racket contact, and the ball was not present in the simulation. The spatial association of the racket-arm trajectory with the ball position are essential for the use of the distal information to anticipate shot direction, as evidenced by the lowest performance of ball occlusion condition in a previous study using natural stimuli (Jackson & Mogan, 2007). Moreover, evidence pointed out that skilled players fixed their gaze toward the proximal regions of the opponent (Ward et al., 2002) and use both proximal and distal cues to anticipate the shot directions (Jackson & Mogan, 2007; Williams et al., 2009). To be noted that our sample of tennis players had a high expertise, so that also LE expertise matched the "skilled player" expertise of previous studies. When using natural stimuli instead of sticks, lower rate of the judgement of the confidence in the decision of the shot direction have been documented for the occlusion of the body with respect to occlusion of distal parts (Jackson & Mogan, 2007), and more accurate anticipatory judgments were done by skilled players when body regions and not racket and arm were expressed with rich graphical definition (Fukuhara et al., 2017).

Observing the post-stimulus ERP temporal and topographical evolution emerging from our findings, the largest scalp potential amplitude modulations occurred in the occlusion conditions

showing the worst performance (i.e., trunk and ball). In the 110-160 ms time window, lower amplitudes of the pP1 and the N1 in the right hemisphere were observed in the trunk occlusion with respect to no occlusion. Previous ERP studies showed that semantic categorization occurs early in visual processing, and affects the N1 component, mainly over the right hemisphere, in response to animate, homomorphic entities with faces and legs (Proverbio et al., 2007; Zani et al., 2015). A body-specific ERP component has been identified as a negative potential peaking between 120 and 200 ms after stimulus onset over electrodes covering the parieto-occipital regions (PO7/PO8). In this kind of task, with human images, this component is assumed to be generated by the extrastriate body area (EBA; Pourtois et al., 2007; Soria Bauser & Suchan, 2013; Thierry et al., 2006), which selectively responds to the observation of bodies or body parts (Downing et al., 2001). This bodysensitive component has often been mixed up with the visual N1 (Downing & Peelen, 2016; Groves et al., 2018; Moreau et al., 2018; Thierry et al., 2006). Interestingly, conditions impairing body recognition (such as inversion) reduce the N1 amplitude (Minnebusch & Daum, 2009). EBA selectively encodes and makes explicit low-level visual features of human bodies, like body shape and posture (Downing & Peelen, 2011). Beyond the visual perception of the body, several functional Magnetic Resonance Imaging (fMRI) studies evidence that EBA represents the body in a dynamic manner (Jeannerod, 2004), integrating multisensory body-related information (Astafiev et al., 2004; Di Vita et al., 2016; Downing et al., 2001, 2006; Kühn et al., 2011; Peelen & Downing, 2005). Accordingly, our results showed that the N1 component is modulated by postural information coming from the human body, so that its amplitude decreases for the occlusion corresponding to the worse performance. Nevertheless, the effect of occlusion on the N1 is a main effect found only for trunk occlusion, but not for ball occlusion, although also for this last an effect on performance measures was found. We cannot exclude that this ERP occlusion effect would have occurred when viewing any occluded human figure, not limited to spatial occlusion in an action anticipation task. Future studies should address this issue with an additional control condition.

Paired to the N1 reduction in trunk occlusion, a lower amplitude of the pP1 component was found. Previous ERP and fMRI studies provided experimental evidence that prefrontal ERPs originates in the bilateral insula (Berchicci et al., 2019; Di Russo et al., 2016; Perri et al., 2014, 2015, 2016, 2018a, 2018b, 2018c; Ragazzoni et al., 2019; Sulpizio et al., 2017). Studies associating the insular activation to the stimulus-response coupling to guide response selection, underline the contribution of the anterior insula in the categorization process (Boettiger & D'Esposito, 2005). (Ploran et al., 2007) found bilateral anterior insula activation when the subjects felt they have identified the item and interpreted the results in terms of focal attention; in other words, the anterior insula implements the process by which information becomes available to awareness. Moreover, several studies showed an activation profile of the insula consistent with the accumulation of sensory evidence (Ho et al., 2012; T. Liu & Pleskac, 2011; Perri & Di Russo, 2017; Ragazzoni et al., 2019). Additional support to the role of the anterior insula in the evidence accumulation process comes from the association of anterior insula activity with the level of uncertainty and difficulty of the discrimination (Lamichhane et al., 2016), which suggests a key role of this region in the process of comparing a stimulus to a decision criterion (Grinband et al., 2006). Within this context, if the anterior insula is involved in the stimulus-response coupling to guide response selection, since the pP1 in trunk occlusion has lower amplitude compared to no occlusion, we can conclude that for this occlusion at the latency between 110 and 160 ms the anterior insula encodes less sensory information for the motor areas to emit the appropriate response.

Furthermore, the amplitude of the pP2 was reduced in both occlusions producing the impaired accuracy and prolonged response times (trunk and ball occlusion). Frontal positive components peaking in the time intervals of the present pP2 and showing different topographies (from frontal-polar to frontal-central) have been previously reported in visual stimulus-response tasks using different experimental paradigms and labels (Berchicci et al., 2016; Darriba & Waszak, 2018; Di Russo et al., 2019; Gajewski et al., 2008; Potts, 2004b; Wild-Wall et al., 2012). In

particular, in discriminative response tasks, a prefrontal P2 (pP2) has been described, reflecting evidence accumulation processes oriented to accomplish stimulus classification (Perri et al., , 2018a; Perri & Di Russo, 2017; Potts et al., 1996; Ragazzoni et al., 2019). In this perspective, the reduced pP2 in both ball and trunk occlusions signals a reduced efficiency in action recognition at this stage of processing.

Finally, we observed a prefrontal negativity from 300 ms until motor responses (pN2). According to previous results (Di Russo et al., 2019), the amplitude increase of this component in trunk occlusion could reflect the insular processing to extract crucial perceptual features for completing the visual-motor integration and correctly perform the motor task. Furthermore, activity in medial prefrontal cortex has been proposed to predict features of visual stimulus processing and behavioral response during anticipation of visual stimuli (Liang & Wang, 2003). Based on these studies, we can conclude that the anterior insula could become more active when the information needed to decide is lacking.

Comparing expert and less expert participants, the only behavioral differences concerned the accuracy, with the former being more accurate than the latter. The lack of significant differences at the response time level may be explained by a ceiling effect due to the long-term training shared by both groups of participants (Ericsson, 2020). At the electrophysiological level, experts showed a larger amplitude of the P3 component over central-parietal areas and the pN2 than less experts. These differences started at around 400 ms and lasted up to the motor response. Enhanced P3 in experts is in line with previous studies in racket sport (Jin et al., 2011; S. Liu et al., 2017; Shangguan & Che, 2018) that read this effect within the context-updating theory, leading to the interpretation that athletes are more prone to recognize and classify the movement patterns during the observation of the to-be predicted action. However, considering that the P3 was unaffected by the occlusions, we suggest a more tactical interpretation (Berchicci et al., 2016; Saville et al., 2011;

Verleger et al., 2005, 2016) proposing that larger P3 in experts indicate a better stimulus-response coupling.

The enhanced pN2 component in expert suggests that expertise may boost the ability in inhibiting useless or distracting information, which is unrelated to anticipation (Liu et al., 2017). In addition, several studies found that sport expertise may increase top-down attentional processing in frontal lobe interpreting it as attentional superiority on skill-related information, despite distractors (He et al., 2018), or as a more intense attentional processing allowing better adaptation of cognitive control to the requested task (Bianco et al., 2017; Sanchez-Lopez et al., 2014, 2016). Moreover, fMRI studies found stronger activation in elite racket sport players with respect to less expert or novices in medial, dorsolateral and ventrolateral frontal cortex (Wright et al., 2010; Xu et al., 2016), in line with present source localization results. Nevertheless, according to previous results (Di Russo et al., 2019), the amplitude increase of the pN2 in experts could reflect enhanced insular processing to complete the sensory-motor representation and to reach accurate performances.

Regarding 2D-3D comparison, 3D stimulus presentation did not improve accuracy in athletes; conversely, the accuracy was higher in 2D than in 3D in the no-trunk condition only. In this regard, literature is controversial: both a lack of differences in the performance between 2D and 3D stimuli (Lee et al., 2013; S. Liu et al., 2017) and a moderate performance improvement of 3D over 2D stimuli (Balkó et al., 2017; Gray, 2017; Put et al., 2014) have been reported. Even though the behavioural results were puzzling and pointed to modality-difference in response time, no differences were observed for the post-stimulus ERP components in the two presentation modalities. Our data could be influenced by the stereoscopic approach to virtual reality employed in the experimental protocol. More immersive technology, as 3D-helmet, visors, or Cave Automatic Virtual Environment, in which images are projected on the walls of a room and the participant is more involved in virtual reality settings, could have induced different results and, thus, should be implemented in future studies. Moreover, although several elements of stimulation mimic real

situation (e.g., tennis hall background, perspective of the camera), a more ecological condition should include the use of large screens for life-size images projection, so that the performer can complete a response that is the same, or as similar as possible, to that produced in the actual performance environment (Broadbent et al., 2015). Another limitation of our study lies in the complete absence of female samples.

Beyond electrophysiological results, the behavioural results of our study may be used to setup ad-hoc training by selecting the fundamental visual cues in perception-action coupling in athletes to improve their ability to predict the action. Improving their perceptual expertise, we can consequently improve their mental processes simulating the production of the action and as a consequence the planning and initiation of an appropriate expert movement response (Fronso et al., 2017).

Cognitive functions, like anticipatory processing, decision-making skills and conflict solving can benefit from sport practice and long-term sport-related training (see Voss et al., 2010 for a review), suggesting a relationship between motor training and cognitive performance. Indeed, elite athletes perform cognitive tasks requiring executive functions with higher proficiency than non-athletes (e.g. Vestberg et al., 2012). According to the cognitive skill transfer theory (Taatgen, 2013), extensive practice of specific skills (such as sport-related skills) improves individual components of cognition, which can also be used outside the specific sport context during not sport-related cognitive tasks (Furley and Memmert, 2011). Other studies have compared the cognitive performance between athletes playing closed- and open-skill sports to explain the differences in executive functions induced by training in a specific sport cathegory (see Bianco et al., 2017). Nevertheless, our data do not allow us to make conclusion on the relationship between sport-related motor training and general cognitive performance, especially because we did not include a general, not sport-related task. We can only conclude that expert tennis players show a better cognitive

performance than less expert tennis players on a sport-specific task, but not on general cognitive tasks, not sport-related.

Conclusion

In conclusion, although the task was not executed in a real environment, present data confirm that the information coming from the trunk and the ball play a crucial role in anticipation in tennis, so that a worst performance is achieved when they are missing. The stimulus information defect, due to the occlusion in which the body information is missing, do not affect early sensory processing, but activity linked to body processing and sensory-motor awareness, i.e., the process by which the observer becomes aware of the possibility to combine the perceptual event with a motor action. For both trunk and ball occlusions, we instead found reduced decisional processes upon action execution following sensory evidence accumulation. Finally, for trunk occlusion we found larger frontal activity, which may be view as increased insular activity to recover and to complete the most correct sensory motor representation. In more experienced players, more accurate performance was associated with increased activity for stimulus-response coupling in parietal areas and for sensory-motor representation in prefrontal cortex.

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TABLE 1

			Occlusion vs No Occlusion				
			Legs	Ball	R&Arm	Trunk	EP vs LEP
Behaviour	ral						
Accuracy		•	_	$\overline{}$	_		
RT				\uparrow	_		
ERP Comp	•						
	Time Interval	Site					
P1 left	80-110 ms	O1	_	_	_	-	-
P1 right	80-110 ms	O2	_	_	_	_	_
pN1	80-110 ms	FPz	_	_	_	_	_
N1 left	110-160 ms	PO7	_	_	_	_	_
N1 right	110-160 ms	PO8	_	_	_	\downarrow	_
pP1	110-160 ms	AFz	_	_	_	\downarrow	_
pP2	160-280 ms	FCz	_	\downarrow	_	\downarrow	_
visual P2	250-350 ms	POz	_	_	_	_	_
pN2	400-500 ms	FpZ	_	_	_	\uparrow	\uparrow
P3	400-500 ms	Pz	_	_	_	_	\uparrow

Summary of the results. The comparison between occlusion conditions and no occlusion and between EP and LEP are shown for each behavioural variables (accuracy and response time, RS) and for each ERP component. For the ERP components, the corresponding time window and electrode are also shown. The symbol "↑" indicates a higher value in the spatial occlusion with respect to the no-occlusion condition or a higher value in EP than in LEP. The symbol "↓" indicates the opposite (lower value in spatial occlusion than in no-occlusion or lower value in EP than in LP). The symbol "—" indicates no statistical difference.

FIGURE CAPTIONS

FIGURE 1

- **A.** Example of spatial occlusion conditions.
- **B.** Example of a single trial. Please note that the pictures of A had the same size of those in B; they were adjusted only for display purposes.

FIGURE 2

- **A.** Mean (95% confidence interval) of accuracy for 2D (left panel) and 3D (middle panel) condition for each spatial occlusion. Stars indicate significance of paired t-test (Bonferroni corrected) between occlusion and the control condition (no occlusion): * p<0.05, ** p<0.005. On the right panel, the mean (95% confidence interval) of accuracy for EP and LEP is shown. Star indicates significant difference between the groups.
- **B.** Mean (standard error) of response time (RT) for 2D (left) and 3D (right) condition for each spatial occlusion. Stars indicate significance of paired t-test (Bonferroni corrected) between occlusions and the control conditions (no occlusion): *p<0.05, **p<0.005.

FIGURE 3

- **A.** Waveform of the grand-average ERPs (average across 2D and 3D modalities) in the time interval from 100 before to 1000 ms after stimulus onset for each spatial occlusion (no legs: cyan, no ball: magenta, no racket and arm: green, no trunk: red, no occlusion: black). A selection of EEG channels where the maximum of the ERP components is present is displayed for convenience.
- **B.** Topography of the grand average of electric potentials in the time intervals considered for ERP analysis. The investigated ERP component are indicated.

FIGURE 4

A. Left panel: The means (and standard errors) of pP1 component amplitude for each spatial occlusion are displayed. Stars indicate significance of paired t-test (Bonferroni corrected) between spatial occlusions and the control condition (no occlusion): * ** p<0.005. Middle panel: Topography of the difference between no occlusion and trunk occlusion in the time intervals where the N1 and the pP1 were evidenced. Right panel: The means (and standard errors) of N1 component amplitude for each spatial occlusion are displayed.

B. Left panel: Topography of the difference between no occlusion and trunk occlusion in the time interval where the pP2 was evidenced. Middle panel: Topography of the difference between no occlusion and ball occlusion in the time interval where the pP2 was evidenced. Right panel: The means (and standard errors) of pP2 component amplitude for each spatial occlusion is displayed. Stars indicate significance of paired t-test (Bonferroni corrected) between spatial occlusions and the control condition (no occlusion): * p<0.05.

FIGURE 5

A. Left panel: Trunk occlusion vs no occlusion difference of mean topography in the time interval corresponding to pN2. Right panel: Mean (standard error) of pN2 component amplitude for each spatial occlusion. Stars indicate significance of paired t-test (Bonferroni corrected) between spatial occlusion and the control condition (no occlusion): * p<0.05, ** p<0.005.

B. Left panel: EP vs LEP difference of mean topography in the time interval corresponding to pN2 and P3. Middle panel: ERP waveforms at Pz channel and Fpz channel are displayed in the time interval -100 ms to 1.0 s for EP (red) and LEP (blue). Right panel: Mean (standard error) of pN2 amplitude and P3 amplitude for EP and LEP. Stars indicate significance of unpaired t-test (Bonferroni corrected) between LEP and EP: * p<0.05, ** p<0.005.

FIGURE 6

Difference of brain source obtained by eLORETA for the comparisons for which the sensor-level analysis revealed significant differences between ERP components. The values were thresholded at 75% of the maximum power values (indicated by 1).