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COGNITIVE NEUROSCIENCE

Action anticipation beyond the action observation network: a functional magnetic resonance imaging study in expert basketball players

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Keywords: action anticipation, motor expertise, motor resonance system, sports

Abstract

The ability to predict the actions of others is quintessential for effective social interactions, particularly in competitive contexts (e.g. in sport) when knowledge about upcoming movements allows anticipating rather than reacting to opponents. Studies suggest that we predict what others are doing by using our own motor system as an internal forward model and that the fronto-parietal action observation network (AON) is fundamental for this ability. However, multiple-duty cells dealing with action perception and execution have been found in a variety of cortical regions. Here we used functional magnetic resonance imaging to explore, in expert basketball athletes and novices, whether the ability to make early predictions about the fate of sport-specific actions (i.e. free throws) is underpinned by neural regions beyond the classical AON. We found that, although involved in action prediction, the fronto-parietal AON was similarly activated in novices and experts. Importantly, athletes exhibited relatively greater activity in the extrastriate body area during the prediction task, probably due to their expert reading of the observed action kinematics. Moreover, experts exhibited higher activation in the bilateral inferior frontal gyrus and in the right anterior insular cortex when producing errors, suggesting that they might become aware of their own errors. Correct action prediction induced higher posterior insular cortex activity in experts and higher orbito-frontal activity in novices, suggesting that body awareness is important for performance monitoring in experts, whereas novices rely more on higher-order decision-making strategies. This functional reorganization highlights the tight relationship between action anticipation, error awareness and motor expertise leading to body-related processing and differences in decision-making processes.

Introduction

Superior action perception and execution as well as anticipation and decision-making skills may underpin the performance of elite athletes (Yarrow *et al.*, 2009; Araújo *et al.*, 2006). Studies indicate that achieving excellence in sports might be related, at least in part, to the fine-tuning of specific anticipatory 'resonant' mechanisms that allow for a more efficient prediction of the consequences of the actions of others (Abernethy & Zawi, 2007; Aglioti *et al.*, 2008; Urgesi *et al.*, 2012).

Expert athletes and novices might differently process perceptual contextual cues. Evidence for this stems from early research on sports psychology suggesting that expert athletes attend to the key features of a scene. Williams & Davids (1998) showed that skilled soccer players anticipate the ball direction and the opponent's action, by fixating the gaze on an unspecified point of the display, allowing the obtention of information concerning both the ball and the ball passer. Other studies showed that expert athletes are better at recognizing and remembering complex action schemes at which they excel when compared with novice athletes and non-athletes (Abernethy, 1990; Allard *et al.*, 1980; Starkes & Allard, 1983; Starkes, 1987). Other studies suggest that visuo-motor experience affords a more effective anticipation perceptual strategy based essentially on the reading of gesture kinematics (Savelsbergh *et al.*, 2002; Williams *et al.*, 2002). Moreover, expert action monitoring abilities contribute to a more effective adjustment of one's own online behavior and error detection abilities (Maidhof *et al.*, 2009).

Neuroimaging studies of the neural correlates of action perception in expert brains have used action observation passive viewing designs (e.g. Calvo-Merino *et al.*, 2005, 2006; Kim *et al.*, 2011; Pilgramm *et al.*, 2010), simulation designs (Cross *et al.*, 2006), and motor

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imagery designs (Chang *et al.*, 2010; Fourkas *et al.*, 2008). To our knowledge, however, only a few studies have investigated action prediction using functional magnetic resonance imaging (fMRI) in athletes during the observation of sports-related movements. Wright *et al.* (2010, 2011) used an occlusion paradigm in fMRI to investigate differences in neural activation during sports anticipation between expert and novice badminton players. Furthermore, Jin *et al.* (2011) used event-related potentials during the viewing of badminton game video clips to identify the neural correlates of the differences between novice and expert levels of action anticipation. Together, and in tune with previous findings, these studies showed more accurate anticipation judgments in experts compared with novices. Moreover, when compared with novices, experts showed enhanced activation in fronto-parietal and temporal areas involved in action observation and action anticipation (Wright *et al.*, 2010, 2011), and two enlarged event-related potential components, a P300 with parietal distribution and a P2 with posterior–occipital distribution possibly related to perceptual learning (Jin *et al.*, 2011). Crucially, many regions outside the two main nodes of the action observation network (AON) (namely the inferior frontal gyrus/ventral premotor cortex and the inferior parietal lobule) have been implicated in both observation and execution of action. Tkach *et al.* (2007) describe single-neuron responses in the monkey primary motor and dorsal premotor cortices in observation and execution of familiar actions. Moreover, human fMRI studies have shown activity during observation and imitation in cortical areas (e.g. the primary visual cortex, cerebellum and parts of the limbic system) originally not believed to contain mirror properties (Molenberghs *et al.*, 2012). Importantly, direct recording of cell activity in the human brain (Mukamel *et al.*, 2010) showed that double-duty neurons involved in action perception and action execution are found in a variety of cortical areas (e.g. medio-temporal cortex, supplementary motor area, hippocampus).

Using fMRI we sought to determine whether the neural signatures of the superior action anticipation abilities of expert athletes were confined to the classical fronto-parietal nodes of the AON or involved areas outside it.

Materials and methods

Participants

Sixteen basketball players (experts) who had been playing for 3–21 years (aged 19–30 years, mean 22.25 years, SD 3.42 years) and sixteen subjects with no motor or visual expertise in basketball (these participants had never played professionally or at an amateur level and did not attend basketball matches or watch them on television) (novices) (aged 19–37 years, mean 27.44 years, SD 4.59 years) participated in this study. All participants were male and right handed. The expert players were recruited from B and C Italian series professional leagues; they trained for a mean of 5.69 h (SD 1.62 h) per week, having played basketball for a mean of 12.09 years (SD 4.71 years). The expert players had thus accumulated around 468–6552 h of practice (mean $\approx$ 3680 h, SD $\approx$ 1759 h) since they had initiated playing. Novices were recruited at the university and hospital campuses.

All participants were native Italian speakers who reported normal or contact lens corrected-to-normal visual acuity in both eyes. Participants gave their written informed consent prior to participating in the experimental tests and received information concerning the experimental hypothesis only after completion of the experimental tests. The procedures, approved by the independent ethics committee of the Santa Lucia Foundation, were in accordance with the ethical standards of the 1964 Declaration of Helsinki. None of the participants had neurological, psychiatric or other medical problems or any contraindication to magnetic resonance imaging.

Stimuli

We digitally recorded 42 movies of a high-performing B series basketball player (second highest club competition in Italian professional basketball) executing free throws to the basket. In 21 movies, the athlete was requested to perform prototypical moves in order to place the ball inside the basket after a clean parabolic shot. In the remaining 21 movies, the athlete was requested to alter the kinematics in such a way that the trajectory of the ball would either fall short of the basket or surpass it. We thus obtained 21 ‘IN’ and 21 ‘OUT’ movies. We then chose a spatial marker from the background – an invisible rectilinear line prolonging the rightmost vertical bar of the third Swedish ladder to the right. All movies were cut at the frame when the center of the ball overlapped this invisible vertical line. Consequently, the outcome of the shots was not presented as the movies ended before the ball hit the basket, fell short of it or surpassed it. The speed of the movies was then reduced to 0.6 : 1 of the natural speed. This transformation was performed as findings from a previous pilot study indicated the need to reduce speed to avoid a floor effect from both novices and expert players. Next, further editing was accomplished by adding a bright blue or bright red layer of color over the extent of the ball at any three consecutive frames, randomly occurring anywhere along the ball trajectory. This created the illusion of a flashing ball in motion. In 11 of the 21 IN movies, the ball flash was red, and in the remaining 10 movies, the ball flash was blue. In a similar vein, in 11 of the 21 OUT movies, the ball flash was blue and in the remaining 10 movies, the ball flash was red. Subsequently, we doubled the number of movies by creating a reverse version of each movie. We thus obtained 21 Forward and 21 Reverse (Control) versions of each ‘IN’ or ‘OUT’ condition, resulting in a total of 84 movie clips. As we chose a precise spatial marker to cut the movies, there were small variations in the duration of each movie. Thus, movie duration ranged from 2248 to 3609 ms (mean 2766.75 ms, SD 338.36 ms). Movie editing, composition and compression were accomplished using VirtualDub v1.3c freeware and Adobe Premiere Pro CS4 software.

All of the above-mentioned movie transformations were performed in order to obtain an action prediction forward condition and a ball-color-change detection, control reverse condition. The former condition required predicting the outcome of a motor action while maintaining visual attention. The latter condition required perceptual and visual attention only. The forward/reverse design was intended to allow a crucial planned contrast whereby blood-oxygenation-level-dependent activation during the Reverse condition would be subtracted from blood-oxygenation-level-dependent activation during the Forward condition. The result of this specific contrast would be related to prediction only and not to visual attention and low-level visual perception. By using the reverse of the forward movies as controls, we were able to match contrast, speed, kinetics, and visual input. Specifically, the participants were asked to predict the outcome of a forward movie condition (IN or OUT) and to identify the color change in the reverse movie condition (RED or BLUE). Presenting the same forward movies and simply asking a different question in the active and control conditions could also have accomplished this – ‘Does the ball go IN or OUT?’ or ‘Does the ball color change to BLUE or RED?’. However, associating action prediction to forward movies and color-change detection to reverse movies allowed the participants to instantly recognize what they had to attend and respond to. We thus kept the two tasks quite distinct and reduced stimulus habituation.

The movie stimuli were presented on a computer screen reflected on a mirror inside the scanner.

Experimental design

All subjects observed forward (F) and reverse (R) versions of the 42 free-throw movie clips ($N = 84$) in each session. Subjects performed a total of four functional 10.17 min sessions, including movie duration, instructions, fixation and null events. After the first two functional sessions, a $\approx$ 10 min magnetization prepared rapid acquisition gradient echo (rapid acquisition with T1-weighted dominance) structural session was performed. The structural session was followed by the remaining two functional sessions. In total, testing lasted 50 min. This interleaved design of functional and structural sessions avoided fatigue and repetition effects. The F clips and control condition (R clips) movies were presented in block design. Each block was initiated by a Forward Instruction or Reverse Instruction screen (10 000 ms) followed by six fixation–event pairs (fixation, 2000 ms; F or R clip, ±2766.75 ms). The F or R clips were randomly allocated and interleaved by a fixation–no clip null event (5000 ms) pair. Hence, a block was made up of a total of seven fixation–event pairs. A session was made up of 14 blocks (7 F blocks interleaved by 7 R blocks). Half of the expert and novice subjects initiated the experiment with an F clip block and the remaining subjects started with an R clip block. In the F condition, the participants were requested to predict the outcome of the throw pressing one of two buttons on a button press (index finger, OUT; middle finger, IN). In the R condition (control clips), the subjects pressed the respective button to report the ball-color change (index finger, RED; middle finger, BLUE). No forced choice was implicated (subjects responded as soon as they felt that they could correctly predict the outcome of the throw, having up to 2000 ms after the end of the movie, corresponding to the subsequent fixation cross screen). All subjects were instructed to respond as soon as they felt confident about their answer. Moreover, they were told that it was important to be quick in responding, but it was more important to answer correctly (Fig. 1).

Scanning procedure and data acquisition

Data were acquired on a three Tesla Siemens Allegra System and standard preprocessing and analyses were performed using statistical parametric mapping (SPM8; Wellcome Trust Centre for Neuroimaging; http://www.fil.ion.ucl.ac.uk/spm) on Matlab (version 7.1, Mathworks). There were four functional sessions. The functional images that were sensitive to blood-oxygenation-level-dependent contrast were acquired by T2*-weighted echoplanar imaging. Each experimental session comprised 256 volumes. For each functional image, Repetition Time was 38×65 ms = 2.47 s, dimensions were $64 \times 64 \times 38$ mm, and voxel size was $3 \times 3 \times 3.8$ mm. For each subject and session, the first four volumes were discarded to allow for T1 equilibration. The remaining 252 volumes were realigned to the first image to correct for phase advance during volume acquisition.

Behavioral data analysis

Response accuracy ('IN' for Forward IN movies, 'OUT' for Forward OUT movies, 'BLUE' for Reverse BLUE movies and 'RED' for Reverse RED movies) and response reaction times were acquired during the scanning sessions. We computed the inverse efficiency score (IES) by dividing, for each condition and in each subject, the mean correct reaction times by the percentage of directionally correct responses, obtaining an index of overall performance (e.g. Rach *et al.*, 2010; Throne, 2006). The IES was introduced by Townsend & Ashby (1983) in order to control for speed–accuracy trade-off effects, by combining accuracy and reaction times in a single measure. Higher scores indicate worse overall performance.

The IESs were entered into two separate repeated-measures ANOVAs (one 2×2 repeated-measures ANOVA with novices and experts as between-group factor, and collapsed IN and OUT F conditions and R condition as within-subjects effects; and one 2×3 repeated-measures mixed-model ANOVA with novices and experts as between-group factor and F IN, F OUT and R conditions as within-subjects effects). The additional distinction between IN and OUT movies was made because specific neural 'error detector' systems have been proposed to be involved in the recognition of actions that may not lead to the desired outcome (for review see Bechtereva *et al.*, 2005). These systems, involving the anterior cingulate cortex, might be differentially attuned and thus contribute to any differential performance in the responses given to IN and OUT movies in novices and experts.

We also computed bivariate Pearson correlations between the number of hours training and the IESs of experts in order to investigate a possible relationship between these two variables.

Blood-oxygenation-level-dependent analysis (planned contrasts)

For each subject, data were best-fit at each voxel by convolving the hemodynamic response function with the time courses of the following eight event types – correct Forward IN trials, correct Forward OUT trials, correct Reverse trials, errors in Forward IN conditions, remaining errors, instructions for Forward conditions, instructions for Reverse conditions, and key press. Instruction events served as baseline and were not computed in the analysis. Moreover, the 'remaining error' events were also not computed due to the scarcity of other error trials not allowing for a robust statistical analysis. At group level, the single-subjects contrast images of parameter estimates were entered into an ANOVA with Conditions (Correct Forward IN/Correct Forward OUT/Correct Reverse/Error Forward IN) as within-subjects variables and Group (experts/novices) as between-subjects variable. Only Forward IN Error trials were computed because not enough errors were made to allow statistical analysis in the remaining OUT conditions. The analysis aimed at determining for each group the brain areas – (i) recruited for action prediction (i.e. Forward Condition–Reverse Condition); and (ii) differently active for correct and error trials (i.e. Correct Forward IN Condition–Error Forward IN Condition; Error Forward In Condition–Correct Forward In Condition). Statistical maps were initially thresholded at voxel level at $P < 0.001$, uncorrected. Results are reported at cluster level $P < 0.05$ [family-wise correction (FWE)]. To explore our main hypothesis of differential brain responses according to expertise level, we investigated the brain areas differently recruited by the two groups in the contrasts mentioned above, i.e. increased activity in the expert group compared with the novice group, and vice versa, in action prediction conditions and in accurate responding. These critical contrasts provide information concerning expert- and novice-specific neural activation during prediction of the outcome of a free throw executed by another player. To ensure that results relate to areas involved in the conditions of interest, statistical maps were masked with the corresponding main effects (averaged activity from both groups at $P < 0.05$, FWE voxel level). Results are reported at voxel level $P < 0.05$ FWE.

Results

Behavioral responses

The IESs were entered into a 2 × 2 repeated-measures ANOVA (Group × Condition). We found a significant main effect of Group ($F_{1,30} = 6.595$, $P = 0.015$) due to a better performance from experts compared with novices (2122.672 vs. 2501.347 ms/percentage of correct responses). We also found a significant main effect of Condition ($F_{1,30} = 211.522$, $P = 0.000$) due to a better performance in Reverse compared with Forward trials (1475.477 vs. 3148.542 ms/percentage of correct responses). Moreover, we found a significant interaction between Group and Condition ($F_{1,30} = 4.338$, $P = 0.046$). Bonferroni corrected *post hoc* tests showed that IESs in Forward trials were significantly smaller in experts compared with novices, i.e. experts outperformed novices in the Forward condition (2839.411 vs. 3457.672 ms/percentage of correct responses; $P = 0.008$). Conversely, Bonferroni corrected *post hoc* tests showed no differences in overall performance between novices and experts in the Reverse condition (1545.022 vs. 1405.932 ms/percentage of correct responses; $P = 0.367$).

It is well known that specific neural processes related to error-related negativity (a component of brain potential activity) are associated with monitoring and compensating for erroneous behavior (Gehring *et al.*, 1993), such as those that are probably associated with the re-enactment of an OUT free throw, during the observation of OUT trials. These neural processes take place in 'error detection systems', which are called into play even when errors are not corrected or in the absence of awareness that an error has been made, in skilled people (Logan & Crump, 2010). As stated above, we decided to investigate the putative differences in performance between Forward IN and Forward OUT trials, because the error detection systems might be differentially attuned and contribute to any differential performance in the correct responses given to IN and OUT trials between novices and experts. Indeed, whereas experts responded accurately to IN movies in 75% of the instances, novices only did so 69% of the time and this difference was not observed in the OUT movies (94% experts vs. 95% novices). In order to statistically analyze the Forward IN, Forward OUT and Reverse conditions overall performance scores, we broke down the collapsed Forward Condition and entered the data in a 2 × 3 repeated-measures ANOVA (Group × Condition) As before, the significant main effect of Group was maintained ($F_{1,30} = 7.730$, $P = 0.009$) due to a better performance of experts compared with novices (2361.585 vs. 2820.122 ms/percentage of correct responses). Again, we found a significant main effect of Condition ($F_{2,60} = 102.722$, $P = 0.000$). Bonferroni corrected *post hoc* tests showed that IESs in Reverse trials were significantly smaller than in Forward OUT trials and, in turn, these were significantly smaller than in Forward IN trials (1475.477 > 2349.918 > 3947.166 ms/percentage of correct responses, all P-values = 0.000). Again, we found a significant interaction between Group and Condition ($F_{2,60} = 3.235$, $P = 0.046$). Bonferroni corrected *post hoc* tests showed that IESs in Reverse trials did not differ between novices and experts (1545.022 vs. 1405.932 ms/percentage of correct responses, $P = 0.367$).

However, the performance of novices was significantly worse than that of experts in the Forward OUT condition (2484.861 vs. 2214.974 ms/percentage of correct responses, $P = 0.011$) and Forward IN condition (4430.483 vs. 3463.849 ms/percentage of correct responses, $P = 0.026$) (see Table 1). Moreover, experts showed a decrease in performance from Reverse trials to Forward OUT trials, and to Forward IN trials (1405.932 > 2214.974 > 3463.849 ms/percentage of correct responses, all P-values < 0.001). Concurrently, novices also presented the same trend, showing better performance in Reverse trials, compared with Forward OUT trials, compared with Forward IN trials (1545.022 > 2484.861 > 4430.483 ms/percentage of correct responses, all P-values < 0.000).

TABLE 1. Behavioral overall performance (IES) in Forward and Reverse tasks

	Conditions			
	Forward	Forward		
Group	IN	OUT	Reverse	Mean
Experts	3463.849** (292.434)	2214.974** (70.320)	1405.932 (107.267)	2361.585 (116.619)
Novices	4430.483** (292.434)	2484.861** (70.320)	1545.022 (107.267)	2820.122 (116.619)
Mean	3947.166** (206.782)	2349.918** (49.724)	1475.477 (75.849)	

IESs (mean reaction time/percentage of correct responses, SEM in brackets) are represented separately for experts and novices as a function of Forward IN, Forward OUT and Reverse conditions. Asterisks indicate significant comparisons (*$P < 0.05$; **$P < 0.001$).

We also investigated the possible impact of the quantity of practice on performance in the expert group. We quantified practice as a function of the number of hours training per week per 52 (number of weeks in 1 year) per number of years in professional training. We then computed bivariate Pearson correlations and found no significant correlations between practice and IES values (all $P > 0.05$), suggesting that the number of hours of practice (at least from 468 h on) had no influence on the players' online predictive overall performance. No other effects were found.

Blood-oxygenation-level-dependent response results

Action prediction

In order to explore the main effect of prediction, we compared trials in the forward conditions with those in the reverse condition. Neural activity was found in the fronto-parietal nodes of the AON in both expert and novice observers (Fig. 2; Tables 2 and 3). The AON has been shown to be associated with bottom-up processes of embodied cognition (for review see Grafton, 2009). Studies indicate that the two main nodes of this network, namely the inferior frontal gyrus/ventral premotor cortex and the inferior parietal lobule, may be involved in predictive simulation of observed actions (Bar, 2007; Kilner *et al.*, 2007; Urgesi *et al.*, 2007a). We also observed, in both groups, activity in the anterior portion of the parietal cortex, in particular in the primary somatosensory cortex (S1), suggesting that motor simulation may imply mapping of specific sensory features of the observed actions (Costantini *et al.*, 2005). Lastly, we found activity in the visual areas, namely the occipital cortex/posterior temporal gyrus bilaterally in the expert group. The investigation of group differences in action prediction indicated increased recruitment of a posterior area of the inferior temporal cortex (50, −66, −6; 44 voxels, $P = 0.044$ FWE) in the expert group compared with the novices (Fig. 2). This cluster overlaps with a higher-order visual area, referred to as the extrastriate body area (EBA), that is selectively involved in processing a variety of body cues (Candidi *et al.*, 2008; Moro *et al.*, 2008; Peelen & Downing, 2005, 2007; Saxe *et al.*, 2006; Urgesi *et al.*, 2007a,b), perhaps including goal-directed body actions (Astafiev *et al.*, 2004). As we had no *a-priori* hypothesis about the involvement of the EBA in the online prediction of an action, we did not perform a functional localizer task to identify this area in each subject. Nevertheless, we masked whole-brain activity with a sphere of 8 mm radius [i.e.

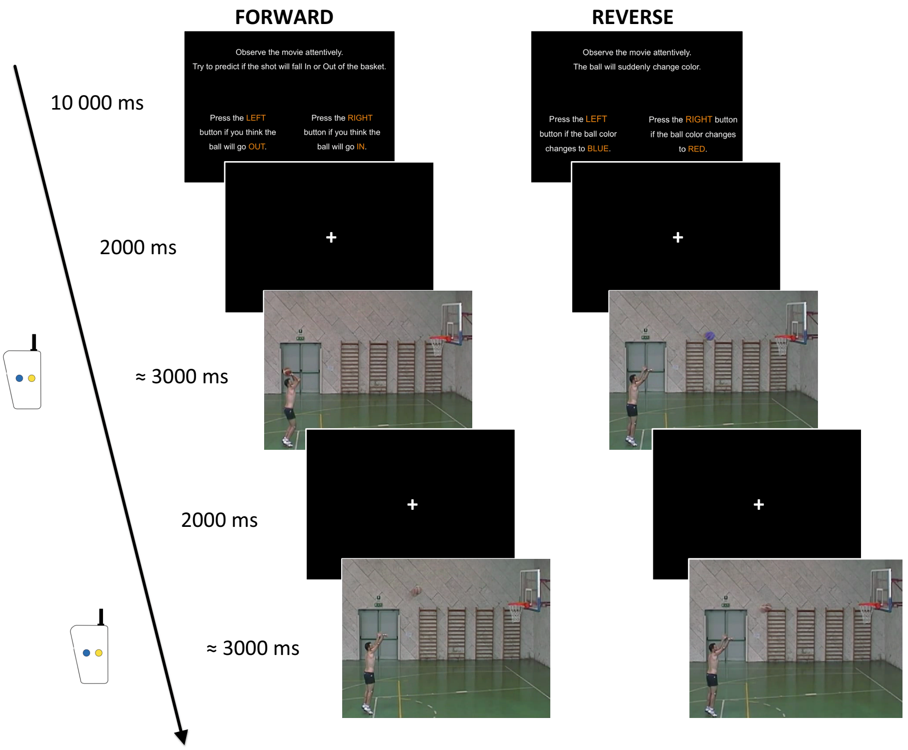

FIG. 1. Study design. Prior to the scanning session, participants were instructed that they should respond as quickly as possible, but only after they were confident of giving a correct answer. Subsequently, and inside the scanner, further instructions (for F or R conditions) were presented onscreen (F instructions: ‘Please attend to the movies displayed and try to predict the outcome of the throws. Use the LEFT button press for predicted OUT shots. Use the RIGHT button press for predicted IN shots.’; R instructions: ‘Please attend to the ball in the movies displayed. At a certain point of the ball trajectory, the ball will change color for a moment. Use the LEFT button press if the color changes to RED. Use the RIGHT button press if the color changes to BLUE.’). After the presentation of the instructions, a series of seven fixation–event pairs (six events + one null event) would appear. Blocks of F and R conditions were presented following a block design.

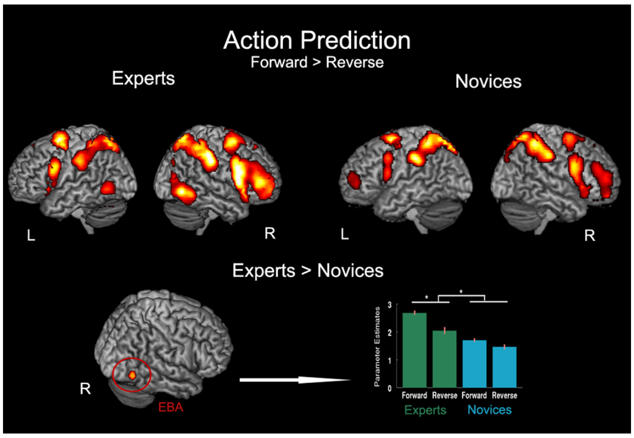

FIG. 2. Brain activations associated with action prediction (i.e. Forward > Reverse). Both expert and novice groups activated areas in the fronto-parietal network associated with action observation and in the postcentral gyrus (somatosensory cortices) when predicting the outcome of an action. The between-groups comparison revealed the additional recruitment of an area within the posterior portion of the inferior temporal cortex, overlapping with the EBA, in experts but not in the novice group. Asterisks indicate significant comparisons ($^*P < 0.05$).

matching the Full Width Half Maximum (FWHM) of the smooth parameters] centered on mean coordinates of peak activity in independent studies (47.6, −69.3, 0.8) (see Moro *et al.*, 2008 for review of these coordinates) and confirmed an overlap between the cluster and the putative EBA area ($t = 4.28$, $P = 0.001$, FWE voxel level). Moreover, we ruled out the possibility that this activity might be due to general movement processing as, according to probabilistic cytoarchitectonic maps (using SPM Anatomy Toolbox V.18), only 4.9% of the reported cluster could be assigned to the motion-sensitive area (MT/hOC5) area (3% of the activated area) (Malikovic *et al.*, 2007). Therefore, it seems that basketball experts, as compared with novices, showed a greater activation of areas involved in visual body processing during the action prediction task, probably reflecting that experts, but not novices, rely on visual body cues to predict the outcome of basket shots performed by others (Abernethy & Zawi, 2007; Aglioti *et al.*, 2008). No significant results were found for the inverse comparison, i.e. greater activations in novices compared with experts in action prediction.

Accuracy-related areas

In the expert group, error trials for out-shot clips were not enough to be entered in a statistical analysis. Interestingly, however, error trials for the in-shot clips (i.e. Error Forward IN movies–Correct Forward IN movies) were associated with activity in the bilateral inferior frontal gyrus (pars orbitalis) and right anterior insular cortex (Fig. 3; Table 4). No significant activity was observed in the novice group. The inferior frontal gyrus has been consistently associated with response inhibition and attentional control (e.g. Aron *et al.*, 2004; Dodds *et al.*, 2011; Hampshire *et al.*, 2010) and the anterior insula with heightened awareness and emotional processing (e.g. Craig, 2009), suggesting that experts but not novices might have become aware of the error.

TABLE 2. Brain areas activated in the expert group for the action prediction contrast

	Action prediction in experts			
	x	*y*	*z*	*t*-value
Parietal cortex				
Right inferior parietal cortex ⁄ supramarginal gyrus	64	−26	38	9.94
Right superior parietal lobe	16	−62	66	8.69
Right postcentral gyrus (BA1 ⁄ BA2)	46	−38	60	7.10
Right supramarginal gyrus ⁄ postcentral gyrus (BA2)	40	−36	44	9.80
Left superior parietal lobe ⁄ precuneus	−16	−62	64	8.37
Left supramarginal gyrus ⁄ inferior parietal cortex	−60	−26	38	7.21
Left inferior parietal lobule ⁄ intraparietal sulcus	−34	−38	44	7.10
Left postcentral gyrus (BA1 ⁄ BA2)	−34	−38	44	6.47
Prefrontal ⁄ frontal cortex				
Right inferior frontal gyrus (BA44 ⁄ BA45)	52	12	12	11.01
Right middle frontal gyrus	48	44	8	8.46
Right superior frontal gyrus	26	6	62	8.66
Left precentral gyrus (BA6)	−54	6	30	7.73
Left inferior frontal gyrus (BA44)	−58	10	26	7.85
Left insular cortex	−30	−20	−4	5.62
Left middle frontal gyrus (BA6)	−24	0	62	10.26
Middle cingulate cortex	4	−4	32	4.50
Temporal cortex, occipital cortex and cerebellum				
Right inferior temporal gyrus (EBA) ⁄ MT ⁄ hOC5	52	−66	−4	9.52
Right middle occipital gyrus	50	−78	12	5.23
Left middle temporal gyrus	−56	−64	−2	5.67
Left cerebellum	−10	−80	−28	7.29

Brain areas activated in the experts group for the action prediction contrast (i.e. Forward > Reverse). Initial activation maps were thresholded at voxel level at $P < 0.001$(uncorrected) and clusters significance set at $P < 0.05$ (FWE-corrected). Coordinates correspond to local maxima of the respective clusters, and are defined in Montreal Neurologic Institute stereotactic space.

However, experts and novices showed a similar activation pattern in the inverse comparison (i.e. Correct Forward IN movies–Error Forward IN movies) (Table 4). Indeed, in both groups, neural activity was found in the putamen and cerebellum, two neural structures that are involved in motor learning and motor control (e.g. Lehéricy *et al.*, 2005; Puttemans *et al.*, 2005; Orban *et al.*, 2010), as well as in somatosensory areas such as the S1. This pattern of results confirms the importance of mapping the motor and sensory qualities of an action to correctly predict the outcome of a fine movement sequence. It is worth noting, however, that for this comparison, activity of the posterior insular cortex was found only in expert subjects and activity of the fronto-orbital gyrus was found only in novices (Fig. 3). Moreover, the posterior insula is part of the interoceptive cortex, and is believed to be intrinsically involved in the representation and somatotopic mapping of sensations from the body (Craig, 2009), suggesting that body awareness mechanisms might come into play when experts make judgments of an action within their expertise. Conversely, the orbito-frontal activity observed in novices seems to suggest the recruitment of upper-level functions to accurately predict the outcome of an action. Thus, it seems that experts and novices might rely on different decision-making strategies for accurate prediction. No significant activity emerged from the between-group analysis in any of the accuracy-related comparisons.

TABLE 3. Brain areas activated in the novice group for the action prediction contrast

Action prediction in novices	*x*	*y*	*z*	*t*-value
Parietal cortex				
Right supramarginal gyrus ⁄ postcentral gyrus (A2 ⁄ A1)	40	−46	60	8.51
Right supramarginal gyrus ⁄ inferior parietal cortex	62	−26	40	8.44
Right superior parietal lobe ⁄ precuneus	14	−68	60	7.79
Left superior parietal lobe	−16	−62	62	10.79
Left inferior parietal lobule	−34	−38	46	9.06
Left supramarginal gyrus ⁄ inferior parietal cortex	−58	−30	38	8.88
Left postcentral gyrus (A1 ⁄ A2)	−40	−46	60	8.51
Prefrontal ⁄ frontal cortex				
Right insular cortex	38	20	0	6.05
Right inferior frontal gyrus (A44)	54	8	26	7.78
Right superior medial gyrus	6	28	46	6.81
Right superior frontal gyrus	26	−4	54	8.41
Right middle orbital gyrus	38	54	−14	5.23
Left precentral gyrus (A6)	−54	6	38	5.69
Left inferior frontal gyrus (A44)	−54	8	18	5.38
Left middle frontal gyrus	−24	0	58	11.15

Brain areas activated in the novice group for the action prediction contrast (i.e. Forward > Reverse). Initial activation maps were thresholded at voxel level at $P < 0.001$(uncorrected) and clusters significance set at $P < 0.05$ (FWE-corrected). Coordinates correspond to local maxima of the respective clusters, and are defined in Montreal Neurologic Institute stereotactic space.

Discussion

Direct recording of cell activity in the monkey premotor and parietal cortex demonstrates the existence of perceptuo-motor neurons during action execution and observation of similar movements made by an experimenter or by conspecifics (mirror neurons) (Fogassi *et al.*, 2005; Gallese *et al.*, 1996). Neuroimaging and neuropsychology studies in humans support the view that the fronto-parietal system, part of the AON, may be fundamental for coupling unimodal and multimodal action perception with action execution (Aglioti & Pazzaglia, 2010, 2011; Pazzaglia *et al.*, 2008a,b). Moreover, studies suggest that recognizing a given gesture (Ogawa & Inui, 2011) performed by others and predicting its outcome (Kilner *et al.*, 2007) might emerge from neural activity in the AON. Relevant to the present research is that most of the studies on action anticipation abilities in experts have focused on the above circuit (e.g. Calvo-Merino *et al.*, 2005, 2006; Cross *et al.*, 2006). Tellingly, however, direct recording of brain activity in monkey (Tkach *et al.*, 2007) and human (Mukamel *et al.*, 2010) brains indicates that neural regions outside this network are involved in both acting and observing actions.

In order to investigate the neural correlates of action anticipation beyond the AON, we performed an fMRI study where expert and novice basketball players determined the outcome of free throws performed by others. Comparing forward and backward action movie conditions allowed us to distinguish predictive action skills and pure attentional monitoring.

Our behavioral results indicate that both expert and novice participants showed better performance in Reverse conditions compared with Forward OUT conditions, which in turn was better than performance in Forward IN conditions. Importantly, expert observers outperformed novices in the Forward online prediction condition, but not in the Reverse control condition. It is possible that OUT shots are more easily anticipated than IN shots, because detecting errors implies a higher amount of certainty than waiting for the error to take place. This result is

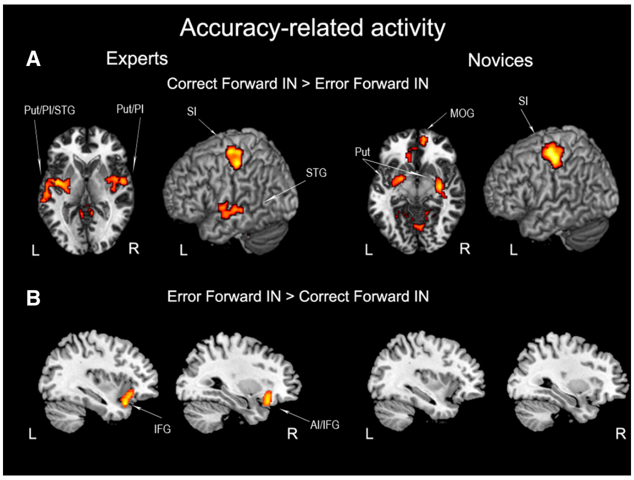

FIG. 3. Brain area-associated accuracy in expert and novice groups. (A) Both experts and novices showed increased activity in the putamen and somatosensory cortices when correctly predicting the outcome of an action (Correct Forward IN > Error Forward IN). However, experts revealed additional activity in the bilateral posterior insular cortices and left superior temporal gyrus, whereas novices recruited areas within the medial orbital gyrus. (B) Only experts showed increased activity associated with poor judgment of the outcome of an action (Error Forward IN > Correct Forward IN) in the bilateral inferior frontal gyrus and right anterior insular cortex. Put, putamen; PI, posterior insular cortex; STG, superior temporal gyrus; MOG, medial orbital gyrus; IFG, inferior frontal gyrus; AI, anterior insular cortex.

TABLE 4. Accuracy-related brain activation

Accuracy-related activity	*x*	*y*	*z*	*t*-value
A				
Left inferior frontal gyrus (pars orbitalis)	−36	18	−20	5.22
Right anterior insular cortex/ inferior frontal gyrus (pars orbitalis)	30	−22	−16	4.98
B				
Left posterior insular cortex/ superior temporal gyrus	−42	−6	4	4.72
Left postcentral/precentral gyrus (A4/A2/A6)	−40	−26	54	5.08
Right posterior insular cortex/ superior temporal gyrus	54	−4	0	4.23
Left putamen	−26	−4	−6	3.71
Left cerebellum	−10	−50	−18	3.91
Right cerebellum	20	−48	−24	5.03
C				
Left precentral/postcentral gyrus (A6/A1)	−46	−16	64	6.02
Left mid-orbital gyrus	−10	54	−12	4.73
Left pallidum/putamen	−22	0	−6	4.53
Right mid-orbital gyrus	10	54	−12	4.73
Right putamen	32	−10	−4	5.60
Right cerebellum	20	−50	−26	5.21

Brain areas showing greater activation – A, when experts made poor judgments (i.e. Error IN > Forward IN); B, when experts made good judgments (i.e. Forward IN > Error IN); C, when novices made good judgments (i.e. Forward IN > Error IN) (no activation was found in the opposite contrast, i.e. Error IN > Forward IN – when novices make poor judgments). Initial activation maps were thresholded at voxel level at $P < 0.001$(uncorrected) and clusters significance set at $P < 0.05$ (FWE-corrected). Coordinates correspond to local maxima of the respective clusters, and are defined in Montreal Neurologic Institute stereotactic space.

in line with our previous research (Aglioti *et al.*, 2008) and with studies showing a relationship between stimulus and response uncertainty (Hong & Beck, 2010). Moreover, expert overall performance in anticipating an action (in the expert's domain of expertise) is superior to that of novices. However, there was no transfer of abilities of this visual predictive competence to other non-related visual detection tasks (Boutin *et al.*, 2011), as suggested by the absence of differences in performance in the Reverse task. It is possible that the superior performance of experts in anticipating the outcome of a free throw might rely on the visual information given by the body cues of the observed player (Aglioti *et al.*, 2008). That the number of hours in practice (at least from 468 h on) was not correlated with the online predictive overall performance of expert players may seem puzzling. However, this result is in keeping with findings showing how physical leisure activity induces training-dependent changes in gray matter after only 40 h of training (Bezzola *et al.*, 2011). Therefore, it is possible that, after a threshold, increased practice will not alter these functional changes but simply maintain them.

Our blood-oxygenation-level-dependent results show that expertise leads to a change of functional activation during action anticipation. In particular, we found neural activity in the fronto-parietal system, part of the AON, in both expert and novice observers alike. This finding confirms previous results showing activation of a shared neural network between action perception and execution. However, we did not find modulation of the activation of the AON with expertise, at least when an anticipation task is involved. Also common to both expert and novice observers was the observation of activity in the S1. It is plausible that motor simulation may imply mapping of specific sensory features of the observed actions (Costantini *et al.*, 2005), independently of expertise. Caetano *et al.* (2007) suggest that the oscillatory activity originating in S1 lasts longer during proper action compared with action observation. The authors go on to suggest that this phenomenon might be linked to proprioceptive signals that occur only during action execution that allow proper agency attribution.

One main point of novelty of the present study is the increased activation in the EBA during the action prediction task as compared with a non-prediction control task, in the bilateral inferior frontal gyrus and the anterior insular cortex during processing of Error Forward IN trials, and the posterior insular cortex during processing of Correct Forward IN trials. This expertise-related, functional reorganization of brain activity is concurrent with a greater performance in action anticipation. Moreover, it may underpin across-group differences in action anticipation, error awareness and decision-making processes.

Here we confirm previous suggestions that motor expertise may lead to body-related processing at an implicit level (Aglioti *et al.*, 2008). Remarkably, we found an increased recruitment of an occipito-temporal region overlapping the EBA in the experts compared with the novices when investigating across-group differences in action prediction. The selective EBA involvement in the visual processing of human bodies has been demonstrated in fMRI (Downing *et al.*, 2001), Transcranial Magnetic Stimulation (Urgesi *et al.*, 2004) and neuropsychological studies (Moro *et al.*, 2008). The EBA was proposed to play a unique role in the perception of action as it computes the static representation of the human body, whereas biological motion is processed elsewhere in the brain. Series of 'snapshot' images of sequential human body postures were proposed to be very informative in terms of the consequential outcome of the action in play (Giese & Poggio, 2003; Downing *et al.*, 2006). Others have defended that the EBA represents dynamic and not static aspects of human motion (Takahashi *et al.*, 2008). It is worth noting that the importance of body-selective regions in action prediction has also been suggested in non-experts who underwent short-term observation of gymnasts' actions (Cross *et al.*, in press).

A study in expert and novice basketball players showed that, although perceptual information may be similarly processed in novices and skilled individuals, the latter can adapt their visual search behaviors, confirming a link between visual search, cognition, and performance (Laurent *et al.*, 2006). The capacity to anticipate and predict another's action or the consequences of the action of another depends on the capacity to read the kinematics of observed actions. Thus, these high-level perceptual capacities are highly intertwined to a motor resonance system between action observation and execution.

Despite similar activation of the AON and S1 between groups, further differences during Forward Error IN trials arose with experts showing a stronger recruitment of the bilateral inferior frontal gyrus (namely the pars orbitalis) associated with response inhibition and attentional control (e.g. Aron *et al.*, 2004; Dodds *et al.*, 2011; Hampshire *et al.*, 2010), and the right anterior insular cortex associated with heightened awareness and emotional processing (e.g. Craig, 2009). These findings showed a differential involvement of the neural system involved in error monitoring and awareness as compared with novices.

The anterior ventral part of the inferior frontal gyrus (pars orbitalis) has been associated with stronger activity during cancelling of hand movements, whereas other regions of the inferior frontal gyrus show stronger activation during the inhibition of eye movements (Leung & Cai, 2007). Such inhibition of motor responses might occur in tandem with awareness of an error committed with the hand. This result may indicate that experts but not novices might have become aware of their own errors. Similar results have already been described in social studies, where the lack of expertise has been suggested to rob the ability to produce correct responses as well as the capacity to surmise that errors are being produced (Dunning *et al.*, 2003).

Further, similar activation in expert and novice participants was observed when considering only the Forward IN trials that were given the correct IN attribution. Both groups showed neural activity in the putamen and cerebellum, two neural structures that are involved in motor learning and motor control (e.g. Puttemans *et al.*, 2005). However, expert-specific and novice-specific activation also survived this contrast with experts (only) showing activity of the posterior insular cortex, part of the interoceptive cortex and novices (only) showing activity of the fronto-orbital gyrus. The additional recruitment of the posterior insular cortex by the experts, and orbito-frontal regions by novices, seems to suggest that the attempt to make accurate predictions might rely preferentially on sensorimotor resonance mechanisms in experts (Aglioti *et al.*, 2008) and on slower upper-level decision-making strategies for accurate prediction in novices.

Taken together, these findings substantiate the existence of an expertise-specific network that is activated during anticipation of observed actions. This network spreads beyond the classical fronto-parietal nodes of the AON system. This pattern of results suggests that expertise does not only arise from the accumulation of experience contributing to strengthen the AON, but also depends on other components that allow for a fine detection of correct body cues, awareness of errors and strong embodiment of the observed action.

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Abbreviations

AON, action observation network; EBA, extrastriate body area; F, forward; fMRI, functional magnetic resonance imaging; FWE, family-wise correction; IES, inverse efficiency score; R, reverse; S1, primary somatosensory cortex.

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