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Action anticipation and motor resonance in elite basketball players

Salvatore M Aglioti[1,2], Paola Cesari[3], Michela Romani[3] & Cosimo Urgesi[4]

We combined psychophysical and transcranial magnetic stimulation studies to investigate the dynamics of action anticipation and its underlying neural correlates in professional basketball players. Athletes predicted the success of free shots at a basket earlier and more accurately than did individuals with comparable visual experience (coaches or sports journalists) and novices. Moreover, performance between athletes and the other groups differed before the ball was seen to leave the model's hands, suggesting that athletes predicted the basket shot's fate by reading the body kinematics. Both visuo-motor and visual experts showed a selective increase of motor-evoked potentials during observation of basket shots. However, only athletes showed a time-specific motor activation during observation of erroneous basket throws. Results suggest that achieving excellence in sports may be related to the fine-tuning of specific anticipatory 'resonance' mechanisms that endow elite athletes' brains with the ability to predict others' actions ahead of their realization.

Although behavioral studies indicate that professional athletes have better sensory and motor skills than novices[1–5], little is known about the neural underpinnings of these superior perceptuo-motor abilities. Moreover, elite sports performance not only involves the ability to execute complex actions such as shooting a ball into a basket, but also the ability to predict and anticipate the behavior of other players. This makes sport practice an excellent opportunity for training the ability to understand the behavior of other individuals. Insights into the neural mechanisms of action understanding come from the discovery of neurons activated during the execution and observation of a given action (the so-called mirror neurons) in the monkey premotor and parietal cortex[6–10]. Neurophysiological[11] and neuroimaging[12–16] studies hint at the existence of motor mirror systems and resonant mechanisms for action also in humans. Transcranial magnetic stimulation (TMS) studies, for example, show that the mere observation of an action induces a selective increase of motor-evoked potentials (MEPs) from the muscles that would be active if the observed actions were performed[17,18]. Moreover, mirror motor activation is greater for 'familiar' than 'unfamiliar' actions[19,20]. In a similar vein, neuroimaging studies show that motor expertise modulates the activation of the human mirror system during the observation of dance moves[21]. Neural activity in premotor and parietal areas was higher in individuals who had direct motor experience of the observed dance moves also when the experimenter controlled for the effect of visual familiarity with the moves[21]. Moreover, learning complex dance patterns modulates neural motor activity during the observation of practiced as compared with visually familiar, but unpracticed, movements[22,23]. Thus, observing others' actions may imply a covert simulation of the very same action, a process probably crucial in both imitative and nonimitative motor learning[24–27]. Modulation of resonant action systems may be important in the superior perceptual abilities shown by athletes engaging in sports activity. It has been shown, for example, that learning to perform new complex action patterns improves the ability to discriminate the same action visually, whether or not visual feedback is present during motor practice[28].

Here we sought to identify the psychophysical and neural mechanisms underlying the highly developed sensorimotor abilities of elite athletes in their domain of expertise by means of two experiments. In the first, three groups of individuals—hereafter referred to as athletes ($n = 10$), expert watchers ($n = 10$, consisting of 5 coaches and 5 sports journalists) and novices ($n = 10$)—were asked to judge the fate of free shots at a basket. In the second, we recorded motor potentials evoked by single-pulse TMS while athletes, expert watchers and novices observed free shots at a basket or soccer kicks at a goal. We tested two predictions: (i) athletes are more accurate in judging the fate of free shots not only with respect to novices, but also compared with expert watchers, that is, individuals who do not play basketball, but observe it as much as athletes; (ii) the higher proficiency of elite athletes parallels an increased excitability of their corticospinal system specifically contingent on observation of basketball, but not soccer actions.

We provide psychophysical and neurophysiological evidence that elite athletes predict the fate of an action by reading body kinematics and that they 'incorporate' fine-grained details of the observed actions. The results indicate that excellence in sports may imply an extremely tight link between embodied mapping and visual readout of observed actions.

[1]Dipartimento di Psicologia, Sapienza Università di Roma, via dei Marsi 78, I-00185, Roma, Italy. [2]Centro Ricerche di Neuropsicologia, Istituto di Ricovero e Cura a Carattere Scientifico Fondazione Santa Lucia, Via Ardeatina 306, I-00179, Roma, Italy. [3]Dipartimento di Scienze Neurologiche e della Visione, Sezione di Scienze Motorie and Facoltà di Scienze Motorie, Università degli Studi di Verona, Via Casorati 43, I-37131, Verona, Italy. [4]Istituto di Ricovero e Cura a Carattere Scientifico 'E. Medea', Polo Friuli Venezia Giulia, via della Bontà 7, I-37078, San Vito al Tagliamento, Pordenone, Italy. Correspondence should be addressed to S.M.A. (salvatoremaria.aglioti@uniroma1.it).

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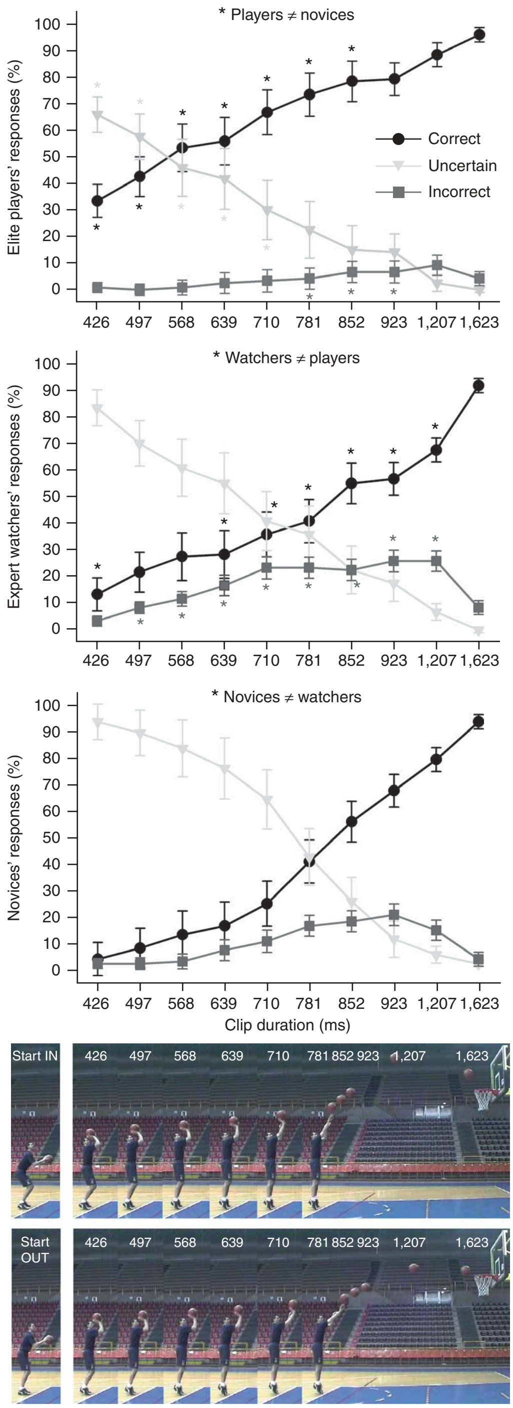

Figure 1 Behavioral data from experiment 1. Percentages of uncertain, correct and incorrect responses (mean ± s.e.m.) made by the elite player, expert watcher and novice groups at the different clip durations. The percentages of uncertain responses indicate the response criterion used by each group. The percentages of correct and incorrect responses indicate the ability of the three groups to predict the fate of the basket shots. Note that the point of intersection between uncertain and correct response curves represents the clip duration at which correct responses were higher than uncertain responses. This occurred after 568 ms for elite athletes, after 710 ms for expert watchers and after 781 ms for novices. Error bars indicate standard errors. Asterisks indicate significant comparisons ($P < 0.05$) between elite athletes and novices (upper graph), between expert watchers and elite players (center graph) and between novices and expert watchers (lower graph).

RESULTS

Experiment 1: psychophysics

In the first experiment we tested whether level of skill in shooting at a basket was correlated with the subjects' ability to predict the outcome of basketball shots observed in a movie. In half of the video clips of free basket shots, the ball landed in the basket (IN shots; **Supplementary Video 1** online), and in the other half the ball landed outside the basket (OUT shots; **Supplementary Video 2** online). We interrupted the complete sequence of each throw at one out of ten possible clip durations. In each trial, we asked participants to press one of three keys on a computer keyboard corresponding to IN, OUT, or 'I don't know' (uncertain) responses. By using a three-choice response we aimed at replicating as closely as possible the type of split-second decisions players face during a game. In fact, when players observe an opponent's shot they may decide to predict the outcome of the shot and thus plan their behavior accordingly, or they may wait for more information. Fast predictions allow anticipating the opponent's behavior, but they imply a higher risk of being wrong and of planning and implementing inappropriate behaviors. On the other hand, choosing to wait allows more accurate, but later, counter-offensives. To catch these subtle aspects of performance, we asked participants to choose one of three possible responses. The percentage of uncertain responses served as an index of the criterion used by the participants to make judgments (**Fig. 1**). Furthermore, both the percentages of correct responses (IN responses for IN shots and OUT responses for OUT shots) and the percentages of incorrect responses (OUT responses for IN shots and IN responses for OUT shots) served as an index of participants' accuracy (**Fig. 1**). We entered the percentages of uncertain, correct and incorrect responses in separate two-way analyses of variances (ANOVAs), with group as between-subjects variable and clip duration as within-subjects variable.

The ANOVA on uncertain responses yielded a significant main effect of clip duration ($F_{9,243} = 82.43$, $P < 0.001$), but not group ($F_{2,27} = 2.11$, $P = 0.141$). However, a significant group × clip duration interaction ($F_{18,243} = 2.1$, $P = 0.007$) suggested that the difference in the behavior of the three groups was modulated by clip duration. Planned comparisons showed that athletes presented a significantly lower number of uncertain responses than novices for the first five clip durations (all P values < 0.05), indicating that novices preferred being uncertain from the very beginning of the action until the 781-ms clip duration. Notably, the 781-ms duration was critical, because at this point the ball left the player's hand and initiated its own trajectory, and no player's influence on the ball trajectory was possible after that instant. Thus, novices tended to be uncertain until they could observe the trajectory of the ball, whereas elite players made IN or OUT predictions even at the shortest clip durations. No significant difference from the beginning to the end of the action was observed between expert watchers and novices (all P values > 0.1) or between expert watchers and elite athletes (all P values > 0.07).

Trend analysis showed that the relation between the percentages of uncertain responses and clip duration was modeled by a linear trend for elite athletes ($F_{1,27} = 54.89$, $P < 0.001$), expert watchers ($F_{1,27} = 83.91$, $P < 0.001$) and novices ($F_{1,27} = 136.74$, $P < 0.001$). This indicates that overall the percentage of uncertain responses in the three groups decreased at longer clip durations. The quadratic trend model was nonsignificant for all groups (all models, $F_{1,27} < 1$). However, although the cubic trend model was nonsignificant for elite athletes and expert watchers (all models, $F_{1,27} < 1$), it was highly significant for novices ($F_{1,27} = 8.85$, $P < 0.006$), showing that the percentage of uncertain responses in novices leveled out at short and long clip durations. Thus, novices made fewer uncertain responses and predicted the shot outcome only when the clips displayed the trajectory of the ball. By contrast, the uncertain responses of elite players and expert watchers decreased linearly with the increase in information conveyed by the longer clips, whether they watched the body kinematics or the ball trajectory. Thus, both expert groups used the same response criterion to predict the fate of the observed shots. Crucially, however, these two groups showed different accuracy in predicting the fate of the shots.

The ANOVA on the percentage of correct responses yielded a significant main effect of group ($F_{2,27} = 6.24$, $P = 0.006$). Pairwise comparisons showed that elite players (66.67%) were significantly more accurate than novices (40.42%; $F_{1,27} = 10.55$, $P = 0.009$) and expert watchers (43.83%; $F_{1,27} = 7.98$, $P = 0.009$). By contrast, the two groups that had no direct motor expertise with basketball did not differ in their ability to predict the fate of the shots ($F_{1,27} < 1$). Therefore, visual expertise did not seem to influence the number of correct responses. The main effect of clip duration ($F_{9,243} = 89.67$, $P = 0.01$) was significant, thus suggesting that the percentage of correct predictions increased with the increase of clip duration. However, the significant interaction group × clip duration ($F_{18,243} = 2.83$, $P < 0.001$) showed that the effect of the superior perceptual abilities of elite players as compared with novices and expert watchers was present only at specific clip durations. Between-group comparisons at each clip duration showed that expert watcher and novice groups never differed from one another (all P values > 0.1). By contrast, athletes made significantly more correct responses than novices at the first seven clip durations (all P values < 0.05). In a similar vein, elite players made significantly more correct responses than expert watchers at all clip durations (all P values < 0.05), except for 497 ms, 568 ms and 1,623 ms (all P values > 0.05).

Trend analysis on the percentage of correct responses showed a significant linear trend for elite athletes ($F_{1,27} = 45.65$, $P < 0.001$), expert watchers ($F_{1,27} = 61.04$, $P < 0.001$) and novices ($F_{1,27} = 112.04$, $P < 0.001$), indicating that overall the percentage of correct responses in the three groups increased at longer clip durations. For elite athletes, however, the quadratic and cubic trend models were nonsignificant (both models, $F_{1,27} < 1$), thus suggesting that elite athletes made more correct responses contingent on the increase of information conveyed in the longer clips, using both body movements and ball trajectory as supplementary cues. By contrast, the quadratic trend model was significant for novices ($F_{1,27} = 5.09$, $P = 0.032$) and marginally significant for expert watchers ($F_{1,27} = 3.63$, $P = 0.067$), implying that the performances of the two groups with no direct motor experience of basketball tended to level out at the first clip durations, but improved greatly when these subjects could rely on ball trajectory. The cubic trend model was nonsignificant for both novice ($F_{1,27} = 1.54$, $P = 0.226$) and expert watcher groups ($F_{1,27} = 2.83$, $P = 0.104$).

The ANOVA on the percentage of incorrect responses showed a significant main effect of group ($F_{2,27} = 6.92$, $P = 0.004$). Pairwise tests showed that expert watchers (16.92%) made significantly more incorrect responses than elite players (3.83%; $F_{1,27} = 13.84$, $P < 0.001$), whereas the difference between expert watchers and novices (10.17%; $F_{1,27} = 3.68$; $P = 0.066$) and between elite players and novices ($F_{1,27} = 3.24$, $P = 0.083$) failed to reach significance. The main effect of clip duration was significant ($F_{9,243} = 16.6$, $P < 0.001$), showing that the percentage of incorrect responses increased as clip duration increased. In particular, when the participants started to make IN or OUT instead of 'I don't know' responses, their error rate increased. Importantly, this pattern differed between the three groups (group × clip duration interaction: $F_{18,243} = 2.06$, $P = 0.008$). Indeed, whereas elite players made only a few incorrect responses (<10%) at all clip durations,

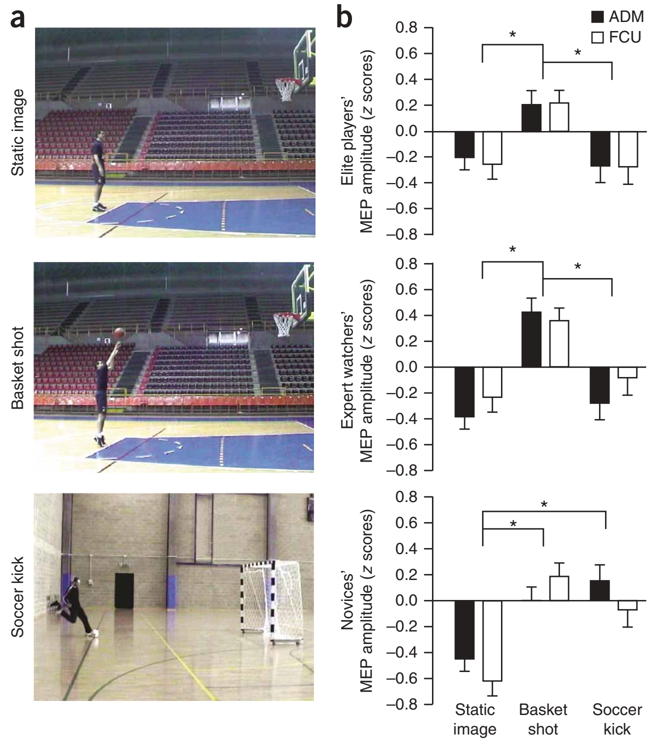

Figure 2 Corticospinal activation during observation of basket and soccer actions. (**a**) Snapshots of three examples of static image, basket shot and soccer kick videos. (**b**) MEP amplitudes (z scores) recorded from the ADM and the FCU in the three observation conditions (basket, soccer and static image) for elite players (upper), expert watchers (center) and novices (lower) groups. Error bars indicate standard errors. Asterisks indicate significant comparisons ($P < 0.05$) between the three observation conditions in each group.

watchers and novices made more errors when the clips lasted more than 639 ms and 710 ms, respectively. Novices made significantly more incorrect predictions than elite athletes when clips lasted from 781 to 923 ms (all P values < 0.05), and expert watchers made more errors than elite athletes at all clip durations (all P values < 0.02) except the shortest and the longest. No difference was observed between novices and watchers (all P values > 0.06). The trend analysis on the percentage of incorrect responses showed no significant trend model for elite athletes (linear: $F_{1,27} = 3.13$, $P = 0.088$; quadratic: $F_{1,27} < 1$; cubic: $F_{1,27} = 1.78$, $P = 0.194$). By contrast, the linear trend model was significant for novices ($F_{1,27} = 8.73$, $P = 0.006$) and expert watchers ($F_{1,27} = 10.96$, $P = 0.003$). Furthermore, significant quadratic and cubic trend models were observed for novices (quadratic: $F_{1,27} = 8.48$, $P = 0.007$; cubic: $F_{1,27} = 20.37$, $P < 0.001$) and watchers (quadratic: $F_{1,27} = 18.77$, $P < 0.001$; cubic: $F_{1,27} = 8.18$, $P < 0.008$). Thus, whereas elite athletes made only a limited number of incorrect responses at all clip durations, novices and expert watchers made a few incorrect responses at the shortest clips. Although it may seem counterintuitive, their error rate increased with longer clips. This effect was due to the increase in error probability related to the change in response from 'I don't know' to IN or OUT. The error rate of novices and expert watchers fell to about zero only at the two longest clips, when the ball was very close to the basket.

Experiment 2: transcranial magnetic stimulation

In the second experiment, we used single-pulse TMS to look for possible relationships between superior perceptual and motor skills and levels of corticospinal motor activity contingent on observation of specific actions. TMS was delivered by means of a figure-of-eight coil positioned on the left primary motor cortex while elite players, novices and expert watchers observed three different types of movies: a basketball player shooting a ball at a basket, a static image of the same basketball player and a soccer player kicking a ball at a goal (**Fig. 2a**). In half of the basketball and soccer movies the ball was IN, and in the other half it was OUT. Moreover, the clips had three different durations: 568, 781 and 1,207 ms. The 568-ms clip displayed only the first phases of the player's movement; the 781-ms clip displayed the player's complete movement until the instant the ball left his hand and began its trajectory; the 1,207-ms clip showed the ball trajectory in addition to what was displayed in the 781-ms clip. In each trial a single magnetic pulse was delivered at a randomly variable interval before the end of the movie. Participants were instructed to keep their muscles relaxed as they watched the movies. They were also instructed to try to predict whether the ball in the basket movies or in the soccer movies was IN or OUT. However, overt reporting was prevented to avoid muscle contractions during MEPs recording. The peak-to-peak amplitude of the MEPs was simultaneously recorded from the hand (abductor digiti minimi, ADM) and forearm (flexor carpi ulnaris, FCU) muscles that are actually involved when the observed action is performed.

We entered mean normalized (*z* scores) amplitude of the potentials evoked from the two muscles in the three different observation conditions (**Fig. 2b**) in a three-way mixed-model ANOVA with group (athletes, watchers and novices) as between-subjects effects and muscle (ADM, FCU) and observation condition (basket shot, soccer kick and static image) as within-subjects effects. The main effect of observation condition ($F_{2,54} = 25.68$, $P < 0.001$) and, more importantly, the interaction observation condition × group ($F_{4,54} = 3.12$, $P = 0.022$) were significant. Within-group comparisons showed that in the elite athletes group MEPs amplitude was higher when observing basket shots (0.22) than soccer kicks (–0.27; $P = 0.017$) and static images of a basketball player (–0.22; $P = 0.028$). There was no difference between the static image and the soccer kick conditions ($P = 0.763$). Thus, watching the basket shot movies was the most activating condition in the elite players group. In the novices group, mean amplitude was lower when observing a static basket scene (–0.53) than when observing shots at a basket (0.01; $P = 0.001$) and soccer kicks at a goal (0.04; $P = 0.003$). We found no difference between basket and soccer movies ($P = 0.69$). Crucially, the pattern of motor facilitation in the watchers group was similar to that in the athletes group, with higher MEPs amplitude during the observation of basket shots (0.39) than during the observation of both soccer kicks (–0.18; $P = 0.002$) and the static image (–0.31; $P < 0.001$), and no difference between soccer and static image conditions ($P = 0.812$). We found no significant MEPs amplitude *z* scores differences between elite athletes and novices (all P values > 0.15), between elite athletes and expert watchers (all P values > 0.22) and between expert watchers and novices (all P values > 0.11) in any of the three observation conditions. Therefore, the effect of selective modulation of corticospinal activation during basket shots observation in visual and motor experts is not due to across-groups differences.

The absence of general differences in neural activation between experts and novices is in keeping with studies showing that motor expertise is linked to a complex reorganization of cortical circuitries that, however, does not necessarily become manifest as simple increase of neural activity[29]. The nonsignificant effect of the three-way interaction ($F_{4,54} = 1.68$, $P = 0.236$) indicates that a similar pattern of results was obtained for MEPs recorded from the ADM and FCU muscles, thus suggesting a nonspecific activation of the cortical representation of the upper limbs muscles. In the novice group the observation of dynamic stimuli induced maximal activation with respect to the static image. Thus, the observation of moving bodies and objects engendered nonspecific activation of the motor system in novices. This may be in accord with psychophysical results indicating that novices can judge the fate of shots at a basket only on the basis of ball-related information. In contrast, in elite athletes and expert watchers we found maximal activation of the motor system during the observation of basketball movies. The two expert groups showed a comparable increase of corticospinal facilitation when they observed basketball-related actions, thus hinting at the equal importance of both motor and visual expertise in modulating the corticospinal motor system. This result may stand in contrast with the psychophysical results of experiment 1, which showed that elite athletes are more accurate not only as compared with novices, but also expert watchers. Moreover, it may stand in contrast with studies showing that, although both physical and observational learning may affect mirror motor mapping of observed actions[23], motor expertise may be more relevant than visual expertise in modulating the frontoparietal mirror system[21–23]. However, our psychophysical results indicate a conspicuously better ability to discriminate IN from OUT shots in elite athletes than in expert watchers. Therefore, we explored further the neural correlates of the higher proficiency of elite players by analyzing MEPs amplitudes during the observation of IN and OUT basket shots at the three clip durations used in experiment 2 (**Fig. 3**).

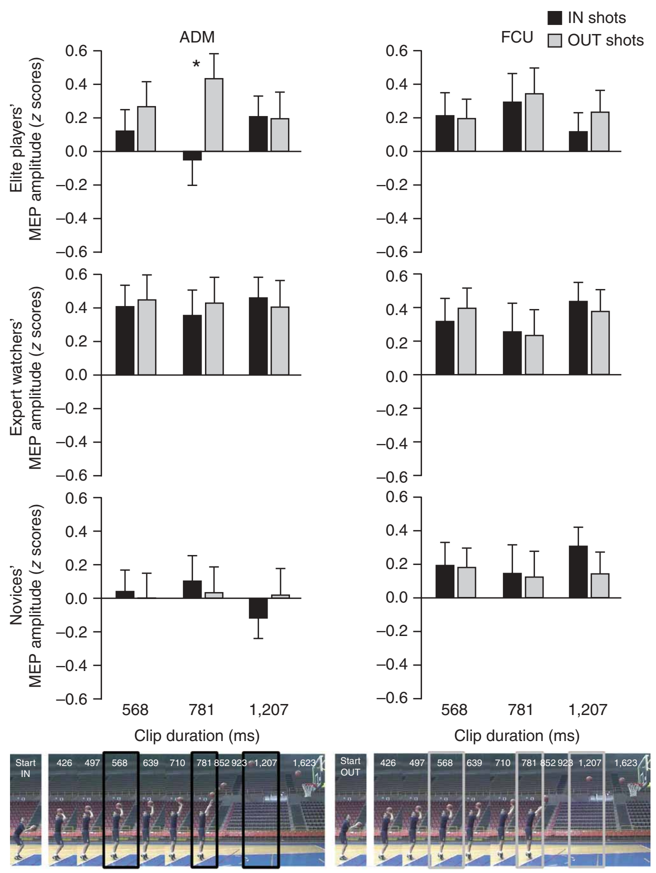

Figure 3 Corticospinal activation during observation of IN and OUT basket shots. MEP amplitudes (*z* scores) recorded from the ADM and the FCU at the three clip durations used in experiment 2. Higher activation during the observation of OUT as compared with IN shots at the 781-ms clip was specifically found in elite athletes. Error bars indicate standard errors. Asterisks indicate significant comparisons ($P < 0.05$) between IN and OUT shots.

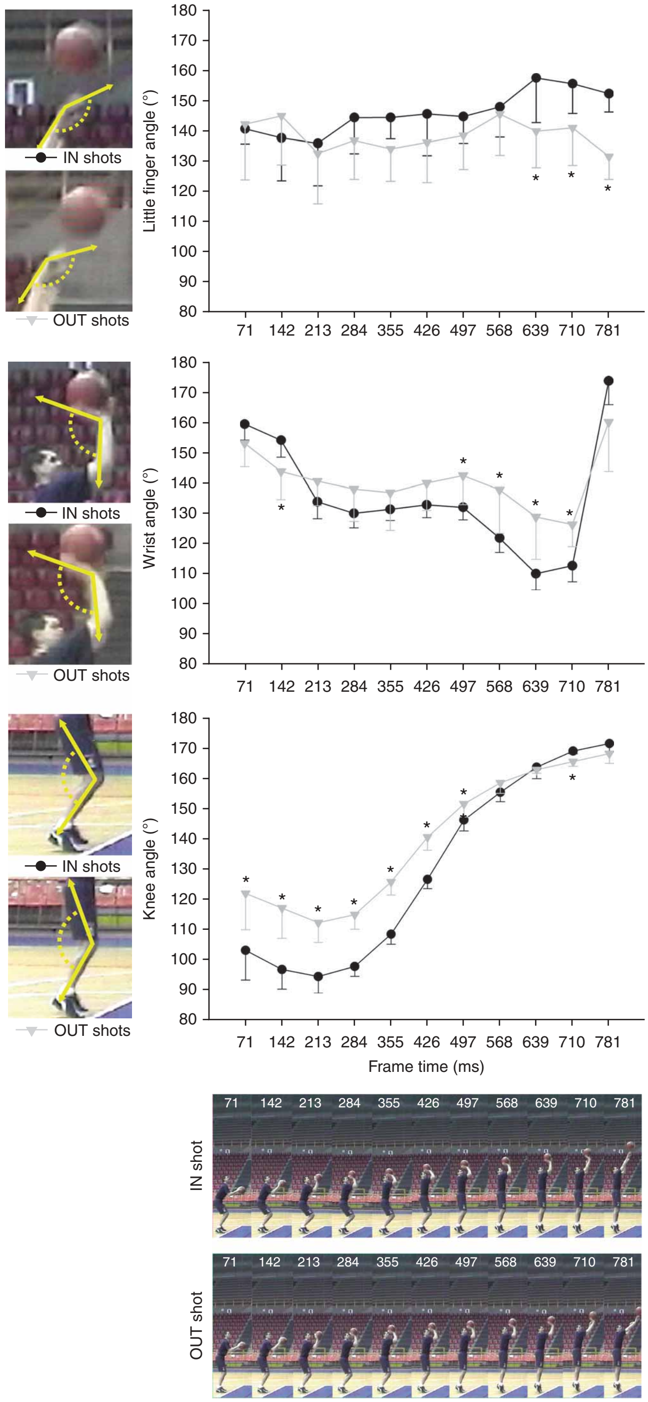

Figure 4 Kinematic analysis of upper and lower limb angle joints. The angles formed by the model's little finger, wrist and knee joints during IN and OUT shots are shown. We measured the angle profiles of each model's joint in the first 11 frames of the IN and OUT shot movies. Each frame was presented for 71 ms. The shortest clip was interrupted after presentation of the first six frames (clip duration = 426 ms). During OUT shots, the extension of the knee was anticipated in the first movement phases, whereas the wrist was less extended between the 639- and the 710-ms clip duration. Note that at the 781-ms clip duration the only difference between the IN and OUT shots was the amplitude of the little-finger angle. Thus, in this phase of the action the fate of the shots was determined by movements of the little finger. Crucially, the between-shot modulation of motor facilitation was observed in the elite players only at this clip duration. Error bars indicate standard deviation. Asterisks indicate significant comparisons ($P < 0.05$) between IN and OUT shots.

We entered normalized MEP amplitudes (z scores) in a mixed-model four-way ANOVA with group (elite athletes, expert watchers, novices) as between-subjects effect and muscle (ADM, FCU), shot (IN, OUT) and clip duration (568, 781, 1,207 ms) as within-subjects effects. Because we found only a significant four-way interaction ($F_{4,54} = 3.31$; $P = 0.017$), we proceeded with two (one for each muscle) follow-up, three-way ANOVAs (group × shot × clip duration). FCU MEPs were not modulated by shot at any clip duration in any group (all F values < 1.1, $P > 0.3$). By contrast, analysis of ADM MEPs showed a significant three-way interaction ($F_{4,54} = 3.28$, $P = 0.018$) indicating a differential modulation related to expertise (group), IN versus OUT throws (shot) and 568-ms, 781-ms, 1,207-ms movies (clip duration). To analyze the source of this three-way interaction we compared MEPs amplitudes by means of three (one for each clip duration) separate two-way ANOVAs with group as between- and shot as within-subjects effect. We obtained no significant main effects or interaction at the 568-ms clip duration (group: $F_{2,27} = 2.82$, $P = 0.077$; shot: $F_{1,27} < 1$; group × shot: $F_{2,27} < 1$). Notably, we found a significant group × shot interaction ($F_{2,27} = 3.9$, $P = 0.031$) at the 781-ms clip duration. Planned between-shots comparisons showed that in elite athletes, corticospinal facilitation was higher during the observation of OUT than of IN shots (0.43 versus –0.05; $F_{1,27} = 11.24$, $P = 0.026$). We observed no significant difference between OUT and IN shots for novices (0.03 versus 0.1; $F_{1,27} < 1$) and expert watchers (0.43 versus 0.36; $F_{1,27} < 1$). The higher motor mapping of observed errors seems to be group- and time-specific, being present only in elite athletes and only during observation of the 781-ms clip, when the movie presentation stopped at the instant the ball left the model's hand. Therefore, this effect may be a neural signature of elite athletes' motor expertise. As a matter of fact, analysis of MEPs recorded from ADM at the 1,207-ms clip duration showed a significant main effect of group ($F_{2,27} = 3.76$, $P = 0.036$), but nonsignificant main effect of shot ($F_{1,27} < 1$) and interaction ($F_{2,27} < 1$). Planned comparisons showed that at 1,207 ms elite athletes and expert watchers had higher MEPs amplitudes than novices ($F_{1,27} = 5.78$, $P = 0.023$). In contrast, watching the 1,207-ms clip, wherein the entire movie sequence was visible, did not induce any significant difference of motor activation between elite athletes and expert watchers ($F_{1,27} = 1.75$, $P = 0.197$). Importantly, the shot success did not modulate this activation, suggesting it may be ascribed to observation of actions belonging to their domain of expertise whether they are motor or visual.

Overall, the IN versus OUT shots analysis shows that a very fine-grained motor facilitation occurred in the group with direct motor experience, but not in the groups with no experience or only visual familiarity with basketball. Indeed, although activation of the motor system during observation of IN and OUT basket shots was observed in all groups, only in elite players was motor facilitation much higher for OUT than IN basket shots. Crucially, this occurred only at the 781-ms clip duration, when the ball left the hand, and the elite athletes' perceptual judgments probably relied on the kinematics of the model's hand movements. Even more important is that this modulation seemed specific for the hand, not the forearm, muscle. One possible explanation for this specificity is linked to the crucial role played by the fingers in exerting the final control on the ball trajectory in the 781-ms clip. This is in keeping with the notion that observation of distal effectors provides fundamental information concerning goal attainment[30]. Note also that the analysis of the kinematics of the joint angles at the different frames composing the IN and OUT shot movies (**Supplementary Note** and **Supplementary Table 1** online) showed that differences between IN and OUT shots regarded mainly lower limbs in the very early frames and upper limbs in the intermediate frames (**Fig. 4** and **Supplementary Fig. 1** online), when the modulation of MEPs recorded from hand muscles was obtained. Crucially, whereas the wrist angle differentiated IN and OUT shots from the 410-ms to the 710-ms clip duration, at the 781-ms duration the little-finger angle was the only kinematics cue for discriminating between IN and OUT shots. The results imply that modulations of TMS indices of excitability of the motor system are closely linked to fine-tuned modulations of behavioral differences in the performance of elite players.

DISCUSSION

The present study explored the neural correlates of the superior perceptual and motor abilities underlying action anticipation in elite basketball players. We provided psychophysical evidence that professional basketball players predict the outcome of free shots at a basket observed on a video earlier and more accurately than people who have no direct motor experience with basketball. Moreover, using TMS we showed an increase of motor excitability in elite athletes when they performed an observational task that tapped the ability to predict the fate of shots at a basket. No such effects were found in a similar task involving soccer kicks. Therefore, the observation-related increase of neuronal activity in the motor system was selective for the observation of highly learned and practiced actions. The psychophysical analysis of the ability to predict the fate of basket shots displayed in clips of different durations indicates that elite athletes probably use body cues to perform the task successfully. By contrast, the predictive abilities of both novices and expert watchers mainly relied on the trajectory of the ball. This pattern of results hints at the importance of motor expertise in the perceptual anticipation of actions performed by other players. Moreover, it expands and complements previous psychophysics research[31,32] on this issue by exploring the influence of visual and motor expertise on action anticipation abilities. We demonstrate a unique role of motor practice in the elite players in addition to the contribution of visual expertise in the expert watchers. It is true that elite athletes and expert watchers used a similar response criterion by making a higher number of IN/OUT responses also during the observation of the shortest clips. This may indicate that both athletes and expert watchers tried to extract relevant information on the fate of the shots by deriving kinematic cues from the model player's body movements. However, expert watchers were less accurate than elite athletes in predicting the fate of the basket shots at the shorter clip durations. Thus, although elite athletes performed better at all clip durations, the greatest differences between the three groups occurred in the early phases of the action, when the ball was still in contact with the hands. This indicates that elite athletes, but not expert watchers or novices, were able to extract relevant information on the fate of the shots at the basket by using kinematic cues from the player's body movements.

The results of the 'I don't know' responses revealed the decision strategy adopted in the three groups. Although novices consistently preferred the uncertain answers at the first five clip durations, elite athletes and expert watchers felt confident of their ability to respond correctly also when only body-action cues were available. However, the expert watchers' accuracy in predicting the fate of shots at the shortest clips was significantly lower than that of elite athletes and not different from that of novices. This indicates that elite athletes, but not novices and expert watchers, can 'read' the kinematics of the observed action. Note that the time spent observing basketball actions was roughly comparable in athletes and expert watchers (7–8 h per week). Moreover, the latter group spent much more time observing basketball than novices; however, the ability to discriminate the fate of basket shots accurately was comparable in novices and expert watchers. Thus, the superior perceptual ability of elite players in anticipating the fate of basket shots may be ascribed specifically to their motor expertise over and above the visual experience that is concomitantly gained during sport performance. Motor control studies indicate that redundant degrees of freedom of body configurations allow accomplishment of the same task by using a range of different kinematic patterns of action[27]. The detection of a biomechanical error adds an additional constraint to this redundancy, thus making easier the prediction of the fate of observed actions. Our results suggest that 'motor' expertise may be crucial for capturing relevant kinematic cues through the readout of nonstandard kinematics from such a redundant system and thus solving even very complex action reading tasks[26,33,34]. Therefore, our psychophysical data provide strong support for direct perception-action mapping hypotheses[19,21,22,24] by showing that seeing without doing is not enough to achieve excellence. Moreover, the data add to the notion of anticipatory action simulation[35,36] by showing that high levels of sports expertise may be related to the anticipatory embodiment of actions.

Our TMS study investigated the neural correlates of sports excellence by measuring the corticospinal excitability of elite athletes, expert watchers and novices while they observed basket shots, soccer kicks and static images. Results showed that corticospinal excitability of both expert athlete and watcher groups increased during the observation of actions belonging to their domain of expertise. By contrast, measures of corticospinal excitability during the observation of soccer kicks were not different from those recorded during the observation of static images of a player. These results suggest that the motor system of elite athletes and expert watchers is activated when they observe actions belonging to their domain of motor or visual expertise. By contrast, in the novice group the observation of moving stimuli induced maximal activation with respect to the static image whether they depicted basket shots or soccer kicks. This may suggest that either motor or mere visual experiences induce increases of corticospinal excitability in keeping with the notion that specific motor learning may derive from purely visual experience[23,27,30,33]. At first sight this result seems to contrast with studies showing that motor expertise may be more relevant than visual expertise in modulating neural activity in the frontoparietal mirror system[21–23]. However, only the elite basketball players presented both a greater ability to predict the outcome of free basket shots and differential excitability of the motor cortex in the conditions in which domain-specific actions performed by others provided cues for fast detection of erroneous performance. Indeed, elite athletes, but not expert watchers and novices, presented higher levels of corticospinal excitability during the observation of OUT as compared with IN shots. Notably, this increase in activity was specific for the hand muscle and only occurred at the instant when, in the OUT shot, the hand-ball contact was crucial for the observers to predict the fate of the player model's shot. We found no specific MEPs modulation during the observation of IN or OUT shots at a basket in expert watchers. Thus, observation of erroneous performance brought about a specific increase of motor facilitation for the elite athlete group, for the hand muscle more directly involved in controlling the ball trajectory and for the instant at which the ball left the hand. This high degree of specificity speaks against the possibility that the effect is due to general emotional reaction to negative outcomes.

The results indicate that although mere visual expertise may trigger motor activation during the observation of domain-specific actions, a fine-tuned motor resonance system subtending elite performance develops only as a consequence of extensive motor practice. Indeed, although the neural systems underlying the matching of observed and executed actions may be early acquired or even innate[37,38], specific learning processes may shape them so as to improve sensorimotor performance[39]. Our study significantly expands previous research by showing that resonant action systems in elite athletes are inherently anticipatory in nature. It also suggests that extremely fine-grained 'perceptual' operations, like early catching of erroneous or ineffective body configurations, are reflected in the modulation of the corticospinal motor system. This is in keeping with studies showing a comparable increase of activation of medial prefrontal and motor areas in the processing of self-generated errors as well as in observing erroneous behavior in others[40,41]. Our results suggest that only motor expertise endows the motor system with the ability to discriminate between erroneous and correct performance. The fine-tuning of these mechanisms may be crucial for the predictive optimal coupling of sensory and motor abilities eventually leading to excellence in many highly complex activities related to motor cognition. The sharing of cognitive and neural codes between perception and action may be crucial for achieving the sensorimotor excellence required by elite athletes.

METHODS

Participants. Ten elite basketball players (elite players) aged 19–28 years (mean = 23.9 years, s.d. = 3.3), five journalists and five coaches (expert watchers) aged 23–46 years (mean = 33.1 years, s.d. = 7.5) and ten students with no experience playing basketball (novices) and aged 18–39 years (mean = 25.4 years, s.d. = 6.8) took part in the study. All participants were men, and all were right-handed according to a standard handedness inventory[42], except for one elite player and one novice, who were left-handed. Elite basketball players were recruited from the Italian Professional League; they trained 7 h (s.d. = 1.7) per week and had played basketball for 12 years (s.d. = 2.9). Professional journalists and basketball coaches observed basketball for 8 h (s.d. = 6.3) per week and had had specific experience with basketball for 17 years (s.d. = 7.5). Coaches had stopped playing basketball 9.4 years (s.d. = 7) before the experimental testing. Because the criterion for inclusion in the study was that the basketball journalists and coaches must be no longer playing basketball at the time of testing, expert watchers were older than elite players (t_{18} = 3.56, P = 0.002) and novices (t_{18} = 2.42, P = 0.026), who, in turn, were age-matched (t_{18} = –0.63, P = 0.537). However, this was not problematic, because the two groups in which we expected higher differences, that is elite players and novices, were similar in age. On the other hand, we expected behavioral performance and neurophysiological data of expert watchers to be either similar to that of novices if visual familiarity with basketball had no influence, or similar to that of elite players if visual familiarity was crucial. All participants were native Italian speakers with normal or corrected-to-normal visual acuity in both eyes and were naive about the purposes of the experiment. Participants gave their written informed consent and received information about the experimental hypothesis only after the experimental tests were completed. The procedures, approved by the local ethics committee, 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 TMS[43]. There were no reports or observations of any discomfort or adverse effects during TMS.

Apparatus, stimuli and procedure. In experiment 1 we presented 12 digitally recorded movies. The movies showed free basket shots performed by a professional basketball player. In six movies the ball landed in the basket (IN shots; **Supplementary Video 1**), and in the other six the ball landed out of the basket (OUT shots; **Supplementary Video 2**). Each movie's duration was 1,623 ms, and we obtained the animation effect by presenting series of 23 single frames, each lasting 71 ms. From each original movie we created 10 clips in which frame presentation was interrupted at 10 different durations. The minimal exposure time for each clip was 426 ms, and the maximal was 1,623 ms. We presented six IN and six OUT shots for each clip duration, thus resulting in 120 trials (12 per cell) for each participant. The order of IN and OUT trials was randomized. Stimulus-presentation timing, electromyographic (EMG) recording and TMS triggering, and randomization were controlled by using E-prime V1.1 software (Psychology Software Tools) running on a personal computer. Participants sat 80 cm away from a 19-in monitor (resolution, 640 × 480 pixels; refresh frequency, 85 Hz), on which videos were presented and subtended a region of 25.7° × 18.5°. In each trial, participants were asked to press with the right index finger one of three keys on a computer keyboard to choose among three possible responses, namely, 'Ball in', 'Ball out' and 'I don't know'.

Experiment 2 presented three different types of videos: 12 IN and 12 OUT basketball shots, as described before (basket shot), 12 IN and 12 OUT soccer kicks at a goal (soccer kick) and 12 static images of a basketball player (static image). The basket shot, soccer kick and static image presentations could last 568, 781 or 1,207 ms. We repeated twice each basket, soccer and static video and presented them in separate blocks of 72 trials in which the order of IN and OUT shots and of clip duration was randomized. We counterbalanced the order of the three blocks among participants. Each participant provided 72 MEPs in the basket and soccer conditions (12 IN shots and 12 OUT shots for each clip duration) and 36 MEPs in the static conditions (12 images for each duration). The total number of trials for each subject was 180. To avoid priming effects that could affect MEPs size, we randomized the instant the TMS impulses were released between 100 and 400 ms before the end of the video presentation. An interpulse interval of at least 10 s was always allowed before the next trial[44]. In the TMS experiment we prevented overt responses to the basket and soccer stimuli so as to avoid muscular contractions that could affect MEPs size. This choice also allowed us to minimize unwanted differences between observation of dynamic basket and soccer stimuli and observation of static images of a still player where no perceptual judgment about the throw fate was possible.

Electromyography recording and transcranial magnetic stimulation. We recorded MEPs simultaneously from the right ADM and FCU, and made EMG recordings through surface Ag/AgCl cup electrodes (1-cm-diameter) placed in a belly-tendon montage. Viking IV electromyography equipment (Nicolet Biomedical) allowed us to perform the amplification, band-pass filtering (20 Hz–3 kHz) and digitization. The sampling rate of the EMG signal was 20 kHz. To make sure there was no unwanted background EMG activity before the magnetic pulse, we had the signal from both muscles displayed additionally in separate channels set at high sensitivity (50 μV). Moreover, during the preliminary session we sent EMG signals to loudspeakers to provide participants with an auditory feedback of their muscle relaxation. Analysis of the maximal EMG amplitude before the TMS pulse showed no modulation of the spontaneous EMG activity during the different observation conditions (**Supplementary Note** and **Supplementary Tables 2** and **3** online).

For focal TMS we used a 70-mm figure-of-eight stimulation coil, connected to a Magstim 200 Rapid (The Magstim Company), producing a maximum output of 2 T at the coil surface (pulse duration, 250 μs; rise time, 60 μs). Placement of the coil was tangential on the scalp, with the handle pointing backward and laterally 45° away from the midline, approximately perpendicular to the line of the central sulcus, inducing a posterior-anterior current in the brain[45,46]. During the recording session the coil's position was over the left motor cortex in correspondence with the optimal scalp position, defined as the position from which MEPs with maximal amplitude were recorded. Participants wore a tightly fitting bathing cap on which the scalp position for stimulation was marked. The experimenter held the coil by hand and continuously checked its position with respect to the marks. We determined the resting motor threshold (rMT), defined as the lowest stimulus intensity able to evoke 5 out of 10 MEPs with an amplitude of at least 50 μV, by using the higher threshold muscle, namely, the FCU. This procedure produced a clear and stable signal from both targeted muscles in all participants. rMT ranged from 48% to 68% (mean = 57.5%, s.d. = 6.9) of the maximum stimulator output in the elite players group, from 34% to 70% (mean = 52.5%, s.d. = 9.9) in the expert watchers group and from 39% to 64% (mean = 53.7%, s.d. = 7.9) in the novices group. There was no observable difference between the rMT of elite players and of expert watchers (t_{18} = 1.45, P = 0.267) and novices (t_{18} = 1.48, P = 0.156), or between the rMT of expert watchers and novices (t_{18} = 0.44, P = 0.667). To record stable MEPs from the two muscles, stimulation intensity during the recording sessions was 130% of the rMT. MEPs peak-to-peak amplitude (in millivolts) was collected and stored on a computer for offline analysis.

Data analysis. To analyze psychophysical data we calculated percentages of uncertain responses, correct responses and incorrect responses. The percentage of the total responses in which participants made 'I don't know' responses indicated the response criterion. Indeed, if participants felt confident in responding they were expected to make less uncertain responses also for clips of short duration. Importantly, this criterion measure may be at least partially independent from the actual proficiency of the participant in predicting the fate of the shots. Thus, as accuracy measures we calculated separately the percentage of trials in which participants made correct or incorrect predictions to IN or OUT shots. In most psychophysical studies subjects must choose between binary options in forced-choice conditions. Here we used a nonstandard psychophysical procedure to replicate the type of decision a player must take while observing another player's action. Indeed, in naturalistic contexts the player has to decide whether the best choice is to predictively anticipate the fate of IN or OUT shots, or to wait for further information.

In experiment 1 we entered the percentage values of uncertain responses and accuracy data in mixed-model ANOVAs with group (elite athletes, expert watchers, novices) as between-subjects effects and clip durations (from 426 to 1,623 ms) as within-subjects effects. Planned tests allowed for the pairwise comparisons between the performances of the three groups at each clip duration. Furthermore, planned polynomial contrasts tested the trend model that best explained the performances of the three groups contingent on clip duration. We tested the significance of the linear, quadratic and cubic models.

In experiment 2 we normalized the raw MEP amplitude values of each participant (z scores) on the total MEPs recorded from each muscle and analyzed them at two different levels. At the first level, we entered individual mean normalized MEPs into a three-way mixed-model ANOVA with group (elite, expert watchers, novices) as between-subjects and muscle (ADM, FCU) and observation conditions (basket shot, soccer kick, static image) as within-subjects effects. The Newman-Keuls post-hoc procedure facilitated pairwise comparisons of normalized MEPs amplitude during the three observation conditions in each group and between the three groups. At the second-level analysis we compared motor facilitation during observation of IN and OUT basket shots by entering normalized MEPs amplitudes into mixed-model, four-way ANOVAs with group (basket shot, soccer kick, static image) as between-subjects and muscle (ADM, FCU), type of shot (IN, OUT) and clip duration (568, 781, 1,207 ms) as within-subjects effects. Follow-up three-way and two-way ANOVAs allowed us to analyze the source of significant four-way or three-way interactions. Planned tests permitted analysis of the source of significant main effects and two-way interactions.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

S.M.A. conceived the study, designed the experiment and wrote the paper. P.C. and C.U. designed the experiment, collected and analyzed the data, and wrote the paper. M.R. collected the data.

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