Cerebral Cortex October 2008;18:2382–2390
doi:10.1093/cercor/bhn005
Advance Access publication February 21, 2008

Kinesthetic Imagery and Tool-Specific Modulation of Corticospinal Representations in Expert Tennis Players

Alissa D. Fourkas[1,4], Valerio Bonavolontà[2], Alessio Avenanti[1,3,5] and Salvatore M. Aglioti[1,3]

[1]Dipartimento di Psicologia, Università degli studi di Roma "La Sapienza," I-00185 Roma, Italia, [2]Dipartimento di Scienze della Salute, Istituto Universitario di Scienze Motorie, I-00194 Roma, Italia and [3]Centro Ricerche Neuropsicologia, Istituto di Ricovero e Cura a Carattere Scientifico Fondazione Santa Lucia, I-00179 Roma, Italia

[4]Current address: Institut für Medizinische Psychologie und Verhaltensneurobiologie, Eberhard Karls Universität Tübingen, D-72074 Tübingen, Deutschland and National Institute of Neurological Disorders and Stroke, National Institutes of Health, Bethesda, MD 20892, USA

[5]Current address: Dipartimento di Psicologia, Università degli studi di Bologna "Alma Mater Studiorum," I-40127 Bologna, Italia and Centro di Studi e Ricerche in Neuroscienze Cognitive, I-47023 Cesena, Italia

Specific physical or mental practice may induce short- and long-term neuroplastic changes in the motor system and cause tools to become part of one's own body representation. Athletes who use tools as part of their practice may be an excellent model for assessing the neural correlates of possible bodily representation changes that are specific to extensive practice. We used single-pulse transcranial magnetic stimulation to measure corticospinal excitability in forearm and hand muscles of expert tennis players and novices while they mentally practiced a tennis forehand, table tennis forehand, and a golf drive. The muscles of expert tennis players showed increased corticospinal facilitation during motor imagery of tennis but not golf or table tennis. Novices, although athletes, were not modulated across sports. Subjective reports indicated that only in the tennis imagery condition did experts differ from novices in the ability to form proprioceptive images and to consider the tool as an extension of the hand. Neurophysiological and subjective data converge to suggest a key role of long-term experience in modulating sensorimotor body representations during mental simulation of sports.

Keywords: athletes, expert-novice differences, mental practice, motor imagery, transcranial magnetic stimulation

Practice with sensorimotor tasks leads to substantive structural (Draganski et al. 2004; May et al. 2007) and functional (Elbert et al. 1995; Pascual-Leone et al. 1995) changes in the brain. These experience-related neuroplastic changes in the motor system may be induced by physical (Classen et al. 1998; Kelly and Garavan 2005), observed (Stefan et al. 2005), and mentally simulated practice (Lafleur et al. 2002; Jackson et al. 2003; Lacourse et al. 2004). Relevant to the present work is that the neural underpinnings of mentally simulated practice overlap at least partially with those involved in action observation and execution (Grezes and Decety 2001).

A second line of investigation relevant to the research we conducted is the incorporation of tools into the body schema. Clinical evidence indicates that both short- and long-term familiarity of specific body parts (e.g., hands) with specific tools or objects may induce their integration into the human body schema (Aglioti et al. 1996; Berlucchi and Aglioti 1997; Pegna et al. 2001; Maravita and Iriki 2004). This tool incorporation may have important functional implications such as, for example, to elongate the hand space representation in brain damaged (Berti and Frassinetti 2000; Farnè and Làdavas 2000; Maravita et al. 2001) and congenitally blind (Serino et al. 2007) individuals. Moreover, there is a positive correlation between previous experience with a tool and increased activation in the motor cortex (Järvaläinen et al. 2004). To the best of our knowledge, however, imagined tool use has not been investigated.

With the aim of exploring the specificity of body corticospinal representation during mental practice associated with long-term experience with a specific tool, we applied single-pulse transcranial magnetic stimulation (TMS) over the left primary motor cortex of expert tennis players and athletic individuals with no specific experience with tennis. Motor-evoked potentials (MEPs) in contralateral hand (first dorsal interosseous, FDI) and forearm (extensor indicis proprius, EIP) muscles were recorded while the 2 groups of subjects mentally rehearsed a tennis forehand, table tennis forehand, or golf drive while specifically focusing on generating a motor image that the tool (racket, paddle, club) was integrated with and thus an extension of the hand. Therefore, the actions include 1 relatively similar and 1 completely dissimilar to the tennis forehand with which 1 group had expertise, and the choice of tools allowed us to manipulate the physical properties of the objects. Tennis and table tennis employ tools highly similar in shape, but not weight or length, that are used to strike a ball in conceptually similar ways during a forehand. Both actions require the use of 1 hand. The shape of a golf club and how it is used to strike a ball (with 2 hands) is entirely different from tennis rackets, and although clubs are almost twice the length of rackets, their overall weights are similar.

Materials and Methods

Participants

Expert (n = 8) and novice (n = 8) tennis players were matched on age and gender (20–33 years; 14 male). The experts compete in category B or C; the category reflects a personnel ranking calculated on the basis of number and level of tournaments and number of victories. Players ranked in the B and C categories typically compete at a national level and may also compete in regional or international tournaments. The experts had mean (M) = 12.4 [standard deviation (SD) = 2.4] years experience and had played 8.3 (3.2) h in the previous 7 days. All novices were athletic, regularly participating recreationally in football (i.e., soccer), weightlifting, kickboxing, or aerobics, or competitively in swimming (master) or football (i.e., soccer) (semiprofessional). Four of the novices have played tennis recreationally (usually in summer), whereas 4 reported having never played. None had trained or competed in tennis, and none had played in the previous 7 days.

Among the 16 participants, only 1 expert tennis player had played golf (twice, 10 years prior), but all participants had played table tennis; responses to "when you last played table tennis" ranged from 2 weeks to 2 years (M = 7 months, SD = 7 months) with frequency described in general terms ("on occasion," "in summer"). Participants were right handed (Briggs and Nebes 1975), neurologically healthy, without psychiatric or other medical disorders, and without any contra-indications to TMS (Wassermann 1998). Procedures were approved by the local ethics committee and were in accordance with the standards of the 1964 Declaration of Helsinki. Written informed consent was obtained from all participants.

Electromyography

MEPs to single-pulse TMS of the left motor cortex were simultaneously recorded from the right FDI and the EIP. Pairs of silver/silver chloride surface electrodes were placed over the muscle belly (active electrode) and over the associated joint or tendon of the muscle (reference electrode). A ground electrode was placed on the right wrist. A CED Power 1401 (Cambridge Electronic Design Ltd, Cambridge, UK) was connected to an Isolated Amplifier System Model D360 (Digitimer Limited, Hertfordshire, UK) and interfaced with CED Spike 2 software. The second-order Butterworth filter was set between 20 and 2500 Hz (sampling rate, 10 kHz). Signals were displayed at a gain of 1000. Auditory feedback of the electromyography (EMG) signals was used to help subjects maintain voluntary muscle relaxation during electrophysiological preparation.

Transcranial Magnetic Stimulation

The optimal scalp position (OSP) for inducing MEPs in the EIP muscle, which also allowed to record stable MEPs in the FDI muscle, was found by moving the coil in steps of 1 cm until the largest MEPs were found and then marked with a pen. The coil was held tangential to the scalp with the handle pointing backward and laterally at 45° from the midline. Resting motor threshold (rMT) was defined as the lowest stimulus intensity to evoke at least 5 out of 10 MEPs with an amplitude ⩾50 μV (Pascual-Leone et al. 1994) in both EIP and FDI. Using the OSP for the less excitable muscle allowed us to rule out that failures to find modulation were due to a nonadequate stimulation of the less excitable muscle.

Mental Practice Manipulation

Mental practice content was specified to increase experimental control as the cognitive and motivational content of self-selected motor images are unconsciously moderated by confidence (Abma et al. 2002) and skill level (Salmon et al. 1994) and are sport (Boyd and Munroe 2003) and situation (Weinberg et al. 2003) specific. A practice situation was specified to prevent experts "pumping up" for competition in the tennis condition. Translations of the condition-specific instructions are reproduced in the Appendix. Subjects repeatedly imagined a sport action per block, with the imagined action self-paced: tennis forehand, table tennis forehand, and golf drive. It was stressed that the tool (racket, paddle, club) was to be considered part of the hand and thus an extension of the body part, focusing the subject's attention on mentally integrating the tool into the body while mentally practicing the action. This point was discussed with each subject prior to proceeding with the block, and all stated they understood the concept. Thus, in contrast to most other TMS motor imagery research, the 2 monitored muscles were involved in imaginary gripping (isometric contraction) of the tool that would be used during the physical execution of the movement (e.g., forehand swing) rather than their primary task of isotonic abduction (FDI) or extension (EIP) of the index finger. Static visual imagery of watching a sunset at the beach was used as a baseline.

Procedure

Participants sat with their right arm and hand resting on a pillow on their lap and kept their eyes closed during imagery. The condition-specific mental practice instructions were read to and verbally clarified with each subject immediately prior to the block (e.g., tennis instructions before the tennis block). Each block began with a computer signal indicating that the participant should begin; 30 s were allowed for the development of the imagery, after which the first TMS pulse was delivered, followed by another pulse every 7 s until 18 pulses were delivered. Imagery (baseline visual imagery or mental practice of the action while focusing on the integration of hand and tool) was continuous throughout the block. Block length (2.6 m) was determined based on pilot testing that indicated mental concentration could not be reliably maintained for longer periods. The baseline was performed as both the first and last block, whereas the mental practice blocks were randomized. An average of 3 m elapsed between conditions.

Three expert tennis players (male, age 26, categories B and C, with 14–20 years experience), different from those who participated in the imagery tasks, took part in a control experiment in which we recorded EMG activity from the FDI and EIP muscles during actual 1) forceful gripping and 2) sport-specific movement execution. The 3 tools weighed as follows: tennis racquet = 300 g; table tennis paddle = 150 g; and golf club = 350 g. During gripping, the players held the tool (tennis racket, table tennis paddle) at the side of their body with their right hand; for golf, the players held the club in front of their body with both hands, keeping the club off of the ground. Participants then alternated simply holding the tool and forcefully gripping the tool, 5 times per tool. During sport-specific movements, subjects alternated holding the tool and using the tool appropriately (tennis forehand, table tennis forehand, golf swing), 5 times per sport. As in the mental practice experiment, the golf swing was 2 handed, and tennis and table tennis were 1 handed.

Subjective Measures

To assess participant's general motor imagery ability, the difficulty with which they formed visual and kinesthetic images of gross actions (e.g., jumping) was measured with an Italian translation of the Movement Imagery Questionnaire—revised (MIQr: Hall and Martin 1997). The scale on the Italian version [very easy (1), easy (2), fairly easy (3), not easy or difficult (4), fairly difficult (5), difficult (6), very difficult (7)] is reversed from the original; it is reliable (Spearman–Brown split-half coefficient = 0.91) and internally consistent (Cronbach alpha of visual subscale = 0.79 and kinesthetic subscale = 0.89).

The experiment was concluded with obtainment of introspective reports of task performance. Subjects described their imagery in each condition to assess compliance with instructions and evaluated their imagery on a series of statements using Likert-type scales. The feedback indicated that both experts and novices used their imagery time complying with the imagery instructions. Subjects found it difficult to control the static visual image for the full length of the block (2.6 m), but reported compliance with the instructions; the imagery was rated "fairly clear and vivid" (median response). There was no reported difficulty with mental practice. All participants used a first-person perspective and imagined all actions in practice settings. Table 1 contains a qualitative summary of the mental practice feedback.

We controlled whether corticospinal excitability reflected the presumed weight of the tool by asking the athletes which tool they thought was heaviest. That is, if subjects incorporated expected tool weight into their motor imagery and increased their imagined muscle tension accordingly, then it would be reasonable to expect the largest MEPs with the heaviest tool (c.f., Gentili et al. 2004). All experts and 6 novices stated that they believed a golf club weighs more than a tennis racket. We also administered a short questionnaire about the use of mental practice in sport (do you use it and if so, for what sport, when, and why?) to ascertain if there were differences among participants in regard to familiarity with this form of practice. One expert tennis player had worked for a short time with a sport psychologist and reported a familiarity with the concept. All participants (novice and expert), however, reported that they did not use mental practice as a form of training. This is unsurprising with our Italian population because, at least for tennis, only the highest level of athletes (i.e., category A) utilize the service of sport psychologists.

Table 1
Summary of introspective reports

	Experts			Novices		
	Tennis	Table tennis	Golf	Tennis	Table tennis	Golf
First person	Completely agree (1)	Agree (2)	Completely agree (1)	Agree (2)	Agree (2)	Agree (2)
Easy to control	Agree (2)	Agree (2)	Agree (2)	Not sure (3)	Agree (2)	Not sure (3)
Extension of hand	Completely agree (1)	Agree (2)	Not sure (3)	Not sure (3)	Not sure (3)	Not sure (3)
Success of hit	100%	99%	70%	97%	95%	65%
Kinesthetic imagery						
Difficulty	Very easy (1)	Fairly easy (3)	Not easy or hard (4)	Not easy or hard (4)	Fairly easy (3)	Not easy or hard (4)
Muscle tension	Not weak or strong (4)	Not weak or strong (4)	Not weak or strong (4)	Fairly strong (5)	Not weak or strong (4)	Not weak or strong (4)
Force behind hits	Fairly high (5)	Not low or high (4)	Fairly high (5)	Fairly high (5)	Fairly high (5)	Fairly high (5)
Frequency of hits	Fairly high (5)	Medium (4)	Medium (4)	High (6)	High (6)	Fairly high (5)
Visual imagery						
Difficulty	Easy (2)	Fairly easy (3)	Fairly easy (3)	Fairly easy (3)	Fairly easy (3)	Fairly hard (5)
Clarity, vividness	Clear (6)	Fairly clear (5)	Fairly clear (5)	Fairly clear (5)	Fairly clear (5)	Fairly clear (5)

The median response per group and condition is identified. Qualitative responses were converted to numerical values for nonparametric analyses. A 5-point scale [completely agree (1), agree (2), not sure (3), disagree (4), completely disagree (5)] was used for 3 statements: whether a first person perspective was always used; the imagined action was easy to control; the tool was sensed as an extension of the participant's hand. Participants reported the percent of imagined hits that they thought had been successful (i.e., were "played" as intended). Remaining statements utilized 7-point scales: difficulty or ease in which the visual and kinesthetic imagery aspects of the mental practice were formed [very easy (1), easy (2), fairly easy (3), not easy/hard (4), fairly hard (5), hard (6), and very hard (7)]; level of imagined muscle tension [very weak (1), weak (2), fairly weak (3), not weak/strong (4), fairly strong (5), strong (6), and very strong (7)]; imagined force behind hits [none (1), very low (2), low (3), not low/high (4), high (5), very high (6), and maximal (7)]; frequency of imagined hits [very low (1), low (2), fairly low (3), medium (4), fairly high (5), high (6), and very high (7)]; clarity and vividness of the visual imagery component [no image seen (1), hazy (2), fairly hazy (3), not hazy/clear (4), fairly clear (5), clear (6), and like real vision (7)].

Data Handling

Background EMG activity was assessed via visual inspection of the data; trials with activity within 100 ms of the TMS pulse, on which movement was observed, or where MEP amplitudes could not be clearly distinguished from background EMG (<0.09 mV) were discarded (8% of trials). Peak to peak millivolts amplitude was calculated off-line using CED Spike 2 software. Outliers (±2 SD) were removed (6% of trials). Raw MEP data from 1 representative expert are presented in Figure 1. Within-group analyses were conducted with repeated measures analysis of variance (ANOVA) on raw amplitudes, as normal distributions were present. Epsilon corrections are reported as Greenhouse–Geisser ($\hat{\varepsilon}$) when Huyht–Feldt ($\tilde{\varepsilon}$) epsilon was less than 0.75. Data for each sport condition were normalized [x − baseline/x + baseline] for analyses with mixed model ANOVA (2 group × 3 sport). Post hoc analyses were computed with the Duncan test. The d statistic was used to compute between-group effect sizes. The statistic, biased by the correlation between 2 items (Morris and DeShon 2002), was modified for within-group analyses (Dunlap et al. 1996). The MIQr was analyzed with t-tests after confirmation of normal distributions. Responses on the Likert-type scales used for the introspective reports were converted to numerical values to analysis. The data were ordinal and analyzed with nonparametric procedures (within: Friedman ANOVA with Wilcoxon-matched pairs post hoc; between: Mann–Whitney U tests).

Control EMG Data

In the control experiment, EMG data were rectified and smoothed and mean waveforms of activity obtained with a 1 s offset. The start and end of each muscle burst was determined by taking a 500 ms window in the 1 s offset, finding the root mean square (RMS) amplitude and calculating 3 SDs of the mean. The point where EMG activity rose above mean + 3 SD was marked as the start of the muscle burst and the point were it dropped below, the end of the burst. Data from the burst were normalized to baseline activity, defined as the activity present during the 500 ms immediately preceding the start of the burst. Raw EMG data from a representative subject are presented in Figure 2.

Results

Preliminary Analyses of MEP Data

There was no between-group difference in rMT, $t(14) = 0.83$, $P = 0.42$ (novice M = 47% of stimulator output, SD = 5%; experts 50%, 7%). Comparisons of MEPs recorded in each muscle of each group during the first and second baseline were nonsignificant (novice FDI $t(7) = 0.13$, $P = 0.90$, EIP $t(7) = 0.61$, $P = 0.56$; expert FDI $t(7) = 1.59$, $P = 0.16$, EIP $t(7) = 1.39$, $P = 0.21$), and the data from the 2 baselines were averaged.

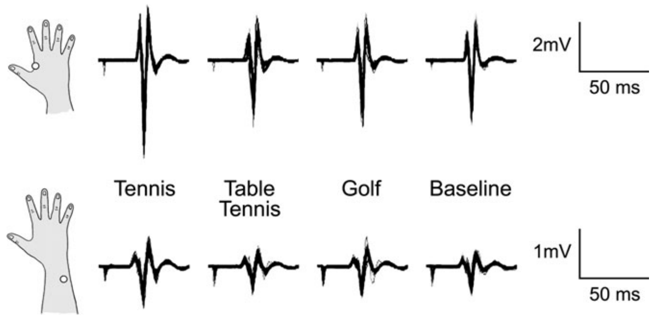

Figure 1. Representative MEP data. Raw MEP data from 1 representative expert tennis player. Peak to peak amplitude traces (18 per sport imagery task, 36 in baseline) are superimposed, with FDI presented in the upper panel and EIP in the lower panel.

Experts

A significant increase in excitability of both hand [$F(3, 21) = 5.54$, $P = 0.010$ for $\tilde{\varepsilon} = 0.82$] and forearm [$F(3, 21) = 5.76$, $P = 0.005$ with $\tilde{\varepsilon} = 1.0$] corticospinal motor representations was detected in expert tennis players (Fig. 1 and Fig. 3*A*). The amplitude of raw MEPs recorded from the hand muscle was significantly higher during mental practice of tennis than during baseline ($P = 0.003$, effect size $d = 0.40$) and table tennis ($P = 0.003$, $d = 0.39$) and tended to be higher during imagery of tennis than during imagery of golf ($P = 0.060$, $d = 0.24$) indicating task-specific tuning of hand motor excitability in expert tennis players. The lack of difference ($P = 0.16$) between MEP amplitudes during golf and table tennis (very different weight) and the higher MEP amplitude during tennis than golf (comparable weight) converge to indicate that the increased amplitudes in tennis are not a function of tool weight per se. Similar findings were observed in the forearm muscle, with higher MEPs during mental practice of tennis than during

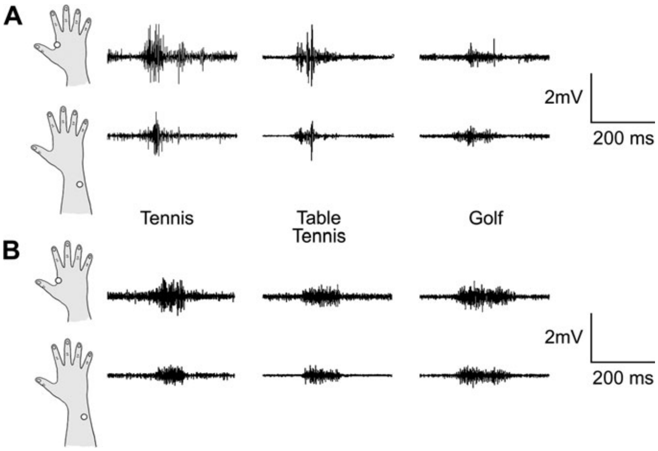

Figure 2. Representative EMG data. Raw EMG data from the hand (FDI) and forearm (EIP) muscle of 1 representative expert tennis player in the control experiment. Data in panel (*A*) illustrate 1 trial recorded during actual swinging of each tool in a task-appropriate manner (tennis forehand, table tennis forehand, golf drive). Data in panel (*B*) illustrate 1 trial recorded during forceful gripping of each tool.

baseline (P = 0.001, d = 0.37) and table tennis (P = 0.034, d = 0.19); MEPs during mental simulation of tennis tended to be higher than during golf (P = 0.067, d = 0.24). Golf elicited higher MEPs compared with baseline (P = 0.049, d = 0.29). MEPs showed a nonsignificant comparison between table tennis and the baseline (P = 0.094). No other significant differences were found in either muscle of experts (FDI $P \geqslant 0.144$; EIP $P \geqslant 0.663$).

Experts' Introspective Reports

In the expert group, the statement "you had the sensation that the tool was an extension of your hand" [$\chi^2(2)$ = 8.10, P = 0.02] revealed more agreement that the tennis racket (rank sum = 11.5) was an extension of the hand than the golf club (20.5), P = 0.03; the rank sum for table tennis was 16.0. The question "you successfully hit what percent" [$\chi^2(2)$ = 8.00, P = 0.02] indicated a higher success rate during imagined tennis (20.0) than golf (12.0) (P = 0.04); the rank sum for table tennis was 16.0. The statement to "rate how hard it was to imagine the physical sensation" [$\chi^2(2)$ = 8.96, P = 0.01] revealed that it was easier to kinesthetically imagine the tennis action (10.5) than the golf action (21.5) (P = 0.02), and tended to be easier than table tennis action (16.0) (P = 0.06). The statement to "rate the force behind your imagined hits" [$\chi^2(2)$ = 8.00, P = 0.02] revealed that the imagined force during table tennis (11.0) was lower than during tennis (20.0) (P = 0.03) and tended to be lower in table tennis than during golf (17.0) (P = 0.07), suggesting that the expert tennis players were attuned to and able to modulate the sensorimotor aspects of the mental practice. The statement to "rate the clarity and vividness of the visual component of your imagery" [$\chi^2(2)$ = 6.33, P = 0.04] revealed tennis imagery (19.5) was more clear and vivid than golf imagery (12.0) (P = 0.04); the rank sum for table tennis was 16.5. Remaining Friedman ANOVAs failed to reach significance (all $P \geqslant 0.22$). Thus, in contrast to the objective measure of MEP amplitude, the subjective data indicated that the imagery consciously experienced during tennis and table tennis was similar, presumably reflecting the similarity in tools and movement (forehand). The objective and subjective data, however, did agree on the lack of difference between golf and table tennis.

Novices

In striking contrast to the expert group, the excitability of novice's hand [FDI: $F(3,21)$ = 1.19, P = 0.337 before epsilon correction] and forearm [EIP: $F(3,21)$ = 2.73, P = 0.123 for $\hat{e}$ = 0.47] corticospinal representations of the hand and forearm muscles was not significantly modulated by different types of mental practice (Fig. 3*B*). The lack of modulation in the raw MEP data was accompanied by sparse significant differences in the subjective feedback; 2 statements on the feedback indicated better quality imagery of table tennis, which all participants had played recreationally on occasion. The statement you had the sensation that the tool was an extension of your hand [$\chi^2(2)$ = 10.10, P = 0.007] revealed more agreement that the table tennis paddle (rank sum = 11.0) was an extension of the hand than the golf club (21.0) (P = 0.03), a tendency toward sensing the paddle was more of an extension than the tennis racket (16.0) (P = 0.07) and for the racket to be sensed as more of an extension than the golf club (P = 0.07). The statement to rate how hard it was to visually imagine the movement [$\chi^2(2)$ = 6.35, P = 0.04] revealed that the table tennis action (11.5) was easier to visualize than golf action (20.0) (P = 0.04), table tennis action tended to be easier than tennis action (16.5) (P = 0.07), and tennis action tended to be easier than golf (P = 0.06). Another statement, to "rate the muscular tension of your imagery" [$\chi^2(2)$ = 6.13, P = 0.05] showed a tendency for lower muscle tension during table tennis action (14.5) than tennis action (20.0) (P = 0.07) and lower muscle tension during golf action (13.5) than tennis action (P = 0.07); remaining Friedman ANOVAs failed to reach significance (all $P \geqslant 0.10$).

None of our novices train with rackets or other tools for their sports, and none of the experts train with paddles or clubs. Nevertheless, it is surprising that there is an absence of clear hand or forearm corticospinal facilitation above baseline in novices and experts for the sports with which they did not have expertise. We believe this may be due to the fact that the monitored muscles were imagined to be under isometric contraction gripping the tool handle, that is, neither muscle was imagined to move. We have previously demonstrated that increased excitability in the motor system is specifically caused by imaging movement of a specific body part, not by generating a mental image of the nonmoving body part per se (Fourkas, Avenanti, et al. 2006; Fourkas, Ionta, and Aglioti 2006). Whereas finding no facilitation in muscles that are not directly involved in the simulated action may be not surprising, the task-specific tuning of motor excitability in expert tennis players may reflect a change in body sensorimotor representations associated with long-term practice.

Experts versus Novices

To directly compare brain activity in the 2 groups, we performed 2-mixed model ANOVAs (2 group × 3 sport), 1 for each muscle, on normalized MEP amplitude values. Analysis for the hand muscle (FDI) showed the tendency for the factor condition [$F(2,28)$ = 3.16, P = 0.069 with $\tilde{e}$ = 0.84]. The factor group clearly failed to reach significance [$F(1,14)$ = 0.59, P = 0.456]. Crucially, the significance of the interaction [$F(2,28)$ = 3.99, P = 0.030] was entirely accounted for by the greater MEP facilitation in experts during mental practice of tennis than the other conditions (Fig. 4*A*): tennis expert_table tennis (P = 0.003, d = 1.12), tennis expert_golf (P = 0.018, d = 0.98),

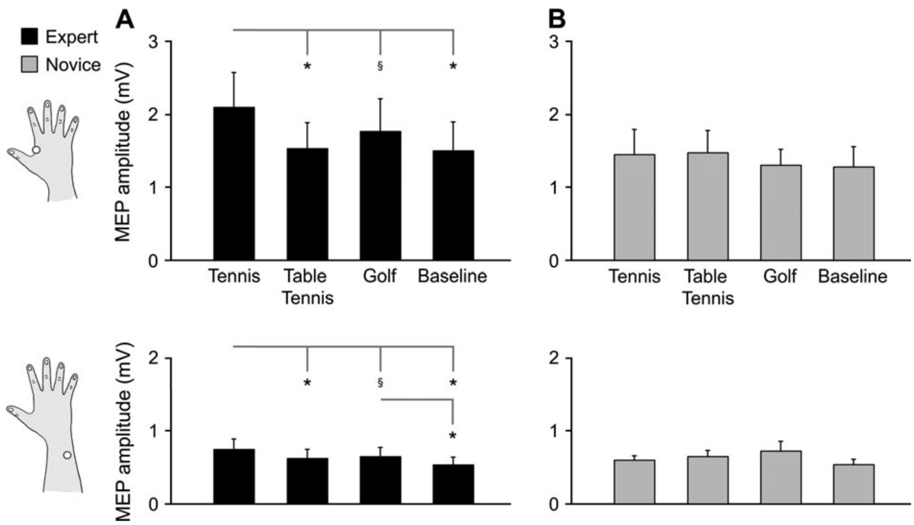

Figure 3. MEP amplitude in the different imagery conditions in the 2 groups. Raw peak to peak amplitude (mean and standard error) in each condition for each muscle. Panel (*A*) depicts data for expert tennis players: in the hand (FDI) muscle mental practice of tennis lead to significant MEP facilitation compared with table tennis and baseline and tended to lead to facilitation compared with golf imagery; in the forearm (EIP) muscle the same pattern was present for tennis, and golf was facilitated compared with baseline. Panel (*B*) illustrates that there were no significant differences in the novice tennis players across conditions in either muscle. $^*P < 0.05$, §$P < 0.07$

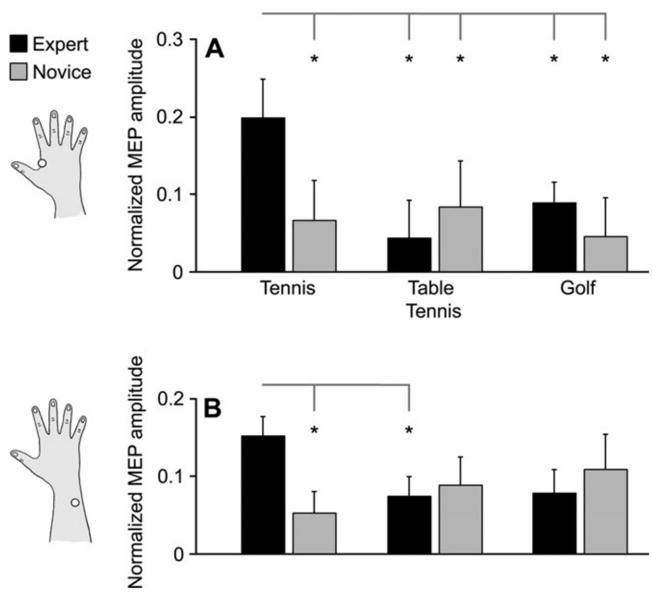

Figure 4. Comparison of groups using normalized data. Means and standard errors are reported. Panel (*A*) shows higher levels of corticospinal facilitation in the hand muscle (FDI) of experts during tennis imagery compared with table tennis and golf imagery and compared with all novice conditions. Panel (*B*) shows higher levels of facilitation in the forearm muscle (EIP) of experts during mental practice of tennis compared with novices and compared with themselves mentally practicing table tennis; experts tended to be facilitated during tennis compared with golf. $^*P < 0.05$

novice_tennis (P = 0.008, d = 0.93), novice_table tennis (P = 0.018, d = 0.75) and novice_golf (P = 0.003, d = 1.10). All other post hoc comparisons were statistically nonsignificant ($P \geq 0.35$). Therefore, the analysis of MEPs recorded from the hand muscle revealed that expert's corticospinal motor system was selectively facilitated during mental practice of tennis in which the athletes concentrated on imaging the tool was integrated with and thus an extension of the hand.

The analysis of the forearm muscle (EIP) showed the insignificance of the factor group [$F(1,14)$ = 0.29, P = 0.602] and condition [$F(2,28)$ = 0.29, P = 0.748]. The interaction, however, was significant [$F(2,28)$ = 3.38, P = 0.049]. The data in Figure 4*B* show that mental practice of tennis in experts elicited greater MEP facilitation in comparison to novice_tennis (P = 0.029, d = 1.26) and tennis expert_table tennis (P = 0.044, d = 0.93); there was a tendency, nonsignificant but with a large effect size, toward higher facilitation for tennis expert_tennis than tennis expert_golf (P = 0.091, d = 0.80). All other post hoc comparisons clearly failed to reach statistical significance ($P \geq 0.16$). This pattern of results further hints at the specificity of the expertise-related effects found in expert tennis players.

Comparisons of the introspective reports of novice and expert tennis players allowed us to investigate whether different qualities of the mental practice may have contributed to the neurophysiological modulation found in the present study. Between-group analyses revealed that experts agreed more than novices that they "had the sensation that the racket was an extension of the hand" [U = 9.5, P = 0.03 (rank sum experts = 45.5, novices = 90.5)], and experts considered it easier than novices "to imagine the physical sensation" (i.e., kinesthetic imagery) during imagery of tennis [U = 9.0, P = 0.03 (rank sum experts = 45.0, novices = 91.0)]. All other comparisons failed to reach significance ($P \geq 0.10$). This suggests that kinesthetic components may have played a role in the different tuning of corticospinal excitability found in expert and novice tennis players during mental rehearsal of tennis. No other comparison, for any sport task, suggested a difference between groups.

Movement Imagery Questionnaire

The link between kinesthetic components and corticospinal modulation was further investigated by asking participants to fill out the MIQr, a standardized motor imagery questionnaire, which assesses subject's ability to form visuomotor and kinesthetic images of one's own body moving. In keeping with previous studies (Atienza et al. 1994; Hall and Martin 1997; Fourkas, Ionta, and Aglioti 2006), kinesthetic imagery was in general more difficult to experience than visuomotor imagery for both experts [kinesthetic M = 9.6 ± 2.7, visual M = 7.9 ± 2.2, $t(7) = 2.70$, $P = 0.031$] and novices [kinesthetic M = 13.9 ± 1.8, visual M = 11.5 ± 1.4, $t(7) = 2.57$, $P = 0.037$]. Moreover, kinesthetic images were more difficult for novices to "feel" [$t(14) = 3.73$, $P = 0.002$], and visuomotor images were more difficult for novices to "see" [$t(14) = 3.88$, $P = 0.002$] indicating that expertise plays a specific role in shaping mental imagery.

To explore the relation between imagery modality and brain activity in the context of motor expertise, we performed a correlation analysis between corticospinal facilitation in the tennis condition and the visual and kinesthetic subscales of the MIQr. When we considered the whole sample ($N = 16$), both visual ($r = 0.52$, $P = 0.039$) and kinesthetic ($r = 0.68$, $P = 0.004$) imagery scores correlated with MEP facilitation recorded from the FDI muscle during mental practice of tennis, with greater corticospinal facilitation associated with better (i.e., easier) imagery (Fig. 5 *A*,*B*; note that for intuitive clarity the data are presented as a positive correlation). Notably, in the expert group, MEP facilitation was strongly associated with the ease of kinesthetic imagery ($r = 0.75$, $P = 0.032$, see Fig. 5*C*), but not with visual imagery ($P = 0.14$). Neither correlation was significant for the novice group. A slight but nonsignificant tendency for better kinesthetic imagery to correlate with increased EIP excitability was present when the whole sample ($N = 16$) was considered ($r = 0.44$, $P = 0.09$), whereas the remaining 5 correlations examined clearly failed to reach significance.

EMG Control Data

EMG was recorded during swinging (subjects alternated holding and using the tool appropriately) and gripping (subjects alternated holding and forcefully gripping the tool) in each of the 3 sports to ascertain if the specific modulation found in our motor imagery task is replicated when the tool is present and used. The absence of a reproduction of the sport-specific modulation found during motor imagery is reported in Table 2. All sports led to increased RMS amplitude in the hand (FDI) and forearm (EIP) muscles during forceful gripping and task-appropriate action.

Discussion

Neuroimaging studies indicate that physical practice with a specific motor task increases neural efficiency of motor areas involved in the task, leading to higher and more focused functional activations during task execution (Kelly and Garavan 2005). Evidence also indicates higher motor activation during mental practice of tasks as a result of short- (Takahashi et al. 2005) and long-term (1 week) physical practice (Lafleur et al. 2002; Lacourse et al. 2005). The present data expand previous findings in the context of long-term extensive experience by showing a selective facilitation of corticospinal motor representations during mental practice of tennis for the group of highly trained tennis players. Importantly, physical training increases the similarity of functional neuroanatomy associated with task execution and task imagination (Lacourse et al. 2005), suggesting that training may also lead to a "better" mental rehearsal of movements associated with the task.

The pattern of relations between brain activity and phenomenological experience suggests that kinesthetic components of imagery may be particularly important in modulating motor excitability during mental rehearsal of movements. Notably, experts also reported that the tennis racket was considered as an extension of the hand and imagined kinesthetic components more easily during tennis mental practice. Thus, the result of a selective corticospinal facilitation for the sport of excellence supports the notion that substantial task experience, involving conscious monitoring such as that present during actual practice, leads to the storage of accurate proprioceptive parameters that can be manipulated via kinesthetic imagery. Although novices considered the table tennis paddle an extension of the hand, the failure to find selective corticospinal facilitation during their mental practice of table tennis may be due to the fact that they only play it recreationally and "on occasion," and hence have not stored accurate proprioceptive information to manipulate mentally. Indeed, although novices generally found the visual components of table tennis easier to imagine than for the 2 other sports, they did not differ across sport actions for the feedback question regarding ease of kinesthetic imagery. This does not imply that motor, tactile, and visual components do not have any influence on motor imagery. What we propose is that the correlation of the MIQr kinesthetic imagery subscale with corticospinal excitability of the tennis players in this study indicates that proprioceptive imagery may play an important role in expert performance.

The correlation can be interpreted in the context of several sports studies, which demonstrate that mental practice incorporating kinesthetic imagery is useful to learning in athletes with expertise in a task, but neither aids nor hinders novice performance (Hardy and Callow 1999). Senior ice skaters find kinesthetic but not visual imagery easier than junior or novice skaters, with the greater ease contributing to more effective mental practice (Mumford and Hall 1985). Roure et al. (1999)

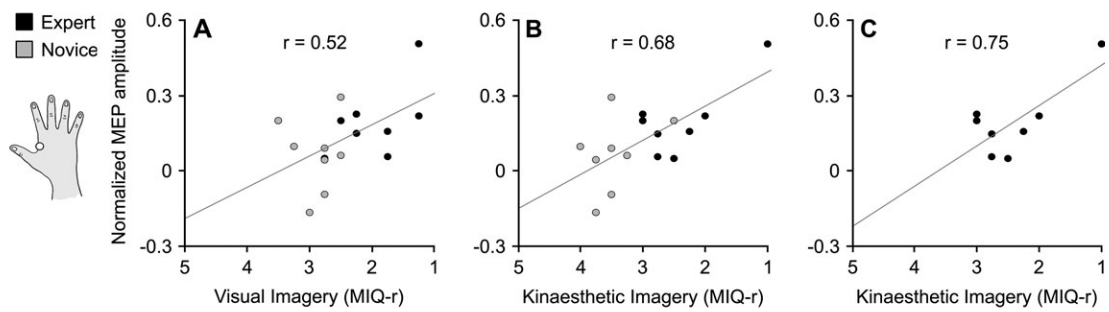

Figure 5. Correlation between MEP facilitation and the MIQr. Scatterplots show significant correlations between corticospinal facilitation in the tennis condition and visual (*A*) and kinesthetic (*B* and *C*) subscales of the imagery questionnaire. The scale on the *x*-axis is reflected for intuitive clarity, making the *r* value positive: 1 indicates a subjective rating of very easy, 2 easy, 3 fairly easy, 4 not easy or hard, and 5 fairly hard.

Table 2
Muscular responses to forceful gripping and task-appropriate action

Task	FDI			EIP		
	Tennis	Table tennis	Golf	Tennis	Table tennis	Golf
Gripping	3.14 (0.69)	2.72 (0.53)	3.05 (0.76)	4.32 (1.45)	2.71 (0.69)	3.93 (1.40)
Swinging	2.76 (0.41)	3.91 (0.89)	2.39 (0.38)	2.74 (0.44)	3.35 (0.87)	2.99 (1.06)

Data for the hand (FDI) and forearm (EIP) muscles are average root mean square (RMS) amplitude of 3 expert tennis players (mean and standard error).

detected a positive correlation between motor imagery (combined visual and kinesthetic), quantified by autonomic responses, and physical performance improvement in intermediate volleyball players mentally practicing receive serve. This evidence, however, does not inform us as to whether better kinesthetic imagery is a result of practice or a cause of excellence. The specificity in corticospinal facilitation for experts we found during tennis imagery supports the notion that the influence of kinesthetic imagery is the result of extensive sport-specific practice; otherwise the greater ease with which experts form kinesthetic images of gross motor tasks, as detected by the MIQr, should have also induced between-group differences in MEP amplitudes during the golf and table tennis conditions. In the present study, expert tennis players exhibited an increase in corticospinal excitability specifically during mental practice of tennis. Differences related to the reported subjective experience primarily reflect better imagery of tennis in experts as compared with golf and table tennis: specifically, the racket was sensed as an extension of the hand, the kinesthetic and visual imagery components were easier to imagine, and the visual imagery was more clear and vivid. The specificity of this pattern precisely mirrors the between-group difference in MEP amplitude detected in both muscles during tennis imagery and the lack of group differences in excitability during golf and table tennis imagery.

Whereas the subjective data clearly suggests that the facilitation in experts may reflect a superior ability to imagine key proprioceptive aspects of the specific task, data from patients (Aglioti et al. 1996; Berlucchi and Aglioti 1997) and blind subjects (Serino et al. 2007) suggest it is also possible that experts have incorporated the tool into their own body schema. Considerable evidence suggests that such incorporations occur in the parietal lobe (Iriki et al. 1996; Moll et al. 2000; Inoue et al. 2001; Obayashi et al. 2001; Obayashi et al. 2002; Ohgami et al. 2004). For example, patients with damage to the right parietal lobe can use tools to temporarily extend the spatial representation of the hand (Berti and Frassinetti 2000; Farnè and Làdavas 2000; Maravita et al. 2001; Pegna et al. 2001; Maravita and Iriki 2004), whereas left parietal damage is implicated in deficits of pantomimed and novel tool use (Goldenberg and Hagmann 1998) and in generating internal models of object-related actions via implicit imagery (Buxbaum et al. 2005). Other evidence shows cerebellar activity changing with purposeful tool use (Imanizu et al. 2000; Obayashi et al. 2002). A limitation of the present study, however, is that the paradigm does not allow us to distinguish in the expert tennis players if the selective corticospinal facilitation is the result of neuroplastic changes that have resulted from extensive training in the sport or extensive use of the tool, as the tool is obviously necessary for the training. Alternatively, both may have contributed. We intend to further explore the issue of incorporation by comparing tool-using expert athlete populations in order to search for more selective motor facilitation.

There are several practical implications of our research. Based on the subjective feedback, which documents adherence to the imagery instructions, we believe that participants accomplished the task we set for them. Specifically, we instructed participants to focus on imaging the tool (racket, club, paddle) was integrated with and an extension of their hand during mental practice. The tool with which each group had the most experience was the tool they most agreed was an extension of the hand—the tennis racket for experts and the table tennis paddle for novices. Moreover, in some cases the participants were not sure if the tool (particularly the golf club, with which everyone had the least—if any—experience) was an extension of the hand. This is in keeping with patient studies suggesting that objects that have been in contact with the body become part of the body schema (Aglioti et al. 1996; Berlucchi and Aglioti 1997) and suggests that using, or imagine using, highly familiar tools may be an effective strategy for reducing deficits in personal and extrapersonal space in brain-damaged patients.

Our expert tennis players utilized their imagery, in particular the kinesthetic aspect, more effectively than novices but only for the activity in which they had expertise. This adds to previous findings which suggest that kinesthetic imagery is helpful during the autonomous stage of motor learning (Hardy and Callow 1999; Cremades 2002). However, this leaves open to future research the question as to whether one should wait until an autonomous stage is achieved to introduce kinesthetic instructions. As modulation of corticospinal excitability occurred only when experts imaged action of the sport they specialize in and kinesthetic imagery correlated more strongly with excitability in experts than novices, it may be relevant to motor rehabilitation to consider if focusing on kinesthetic information too early may be an ineffective strategy and therefore an inefficient use of time. All in all, our neurophysiological and subjective data converge to suggest a key role of long-term experience in modulating sensorimotor body representations during mental simulation of sports.

Funding

Ministero Istruzione Università e Ricerca to S.M.A.; Finanziamento Italiano Ricerca di Base (RBNE01SZB4), University of Rome "La Sapienza"; Fondazione Santa Lucia, IRCCS Roma, Italy.

Notes

Thanks are due to Dr Matteo Candidi for his help. *Conflict of Interest*: None declared.

Address correspondence to Alissa D. Fourkas, Institut für Medizinische Psychologie und Verhaltensneurobiologie, Eberhard Karls Universität Tübingen, Gartenstrasse 29, D-72074 Tübingen, Deutschland. Email: alissa-dora.fourkas@uni-tuebingen.de; fourkasa@mail.nih.gov.

Appendix. Translation of imagery instructions

Instructions were both read to and discussed with participants.

Tennis: "Imagine yourself on a tennis court in a practice session (try to focus on only your half of the court) while playing a forehand shot, repeated several times. The shot should be well played, hit in center of strings, and played with the correct speed and correct angle you have decided on. Try to feel the grip of your hand on the racket handle, as if the racket is the natural extension of your arm, and the racket and hand are integrated into one thing."

Golf: "Imagine yourself on a golf course in a practice session. You are at the teeing-off area having the starting shot. The shot should be a long shot, well played, and with the correct direction which easily reaches the green. Imagine yourself having this shot replayed several times. Try to focus on the feel of your hands holding the handle of the club, as if the club is the natural extension of your arm, and the club and hand are integrated into one thing."

Table tennis: "Imagine yourself playing table tennis in a practice session (try to focus on only your half of the table) while playing a forehand cross table shot, repeated several times. The shot should be well played, with the correct angle and depth you have decided on, but not a smash shot. Try to focus on the feel of the grip of your hand over the handle, as if the paddle is the natural extension of your arm, and the paddle and hand are integrated into one thing."

Baseline: "Imagine yourself on a beach, standing on the sand in front of the sea while watching a beautiful sunset. The beach should be empty, with no people or animals moving around."

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