Somatotopic Mapping of Piano Fingering Errors in Sensorimotor Experts: TMS Studies in Pianists and Visually Taught Musically Naïves

Matteo Candidi1,2, Lucia Maria Sacheli1,2, Ilaria Mega1 and Salvatore Maria Aglioti1,2

1Department of Psychology, University of Rome “Sapienza”, Rome I-00185, Italy and 2IRCCS, Fondazione Santa Lucia, Rome I-00179, Italy

Address correspondence to: Matteo Candidi, via dei Marsi 78, I-00185, Rome, Italy. Email: matteo.candidi@uniroma1.it.

Virtuoso musical performance requires fine sensorimotor skills and high predictive control of the fast finger movements that produce the intended sounds, and cannot be corrected once the notes have been played. The anticipatory nature of motor control in experts explains why musical performance is barely affected by auditory feedback. Using single-pulse transcranial magnetic stimulation, we provide evidence that, in expert pianists (Experiment 1), the observation of a mute piano fingering error induces 1) a time-locked facilitation of hand corticospinal representation which occurred 300 and 700 ms but not 100 ms after error onset, and 2) a somatotopic corticospinal facilitation of the very same finger that commits the error. In a second experiment, we show that no corticospinal modulation is found in non-pianist naïve individuals who were experimentally trained to visually detect the observed fingering errors (Experiment 2). This is the first evidence showing that the refined somatosensory and motor skills of musicians exceed the domain of individual motor control and may provide the brain with fine anticipatory, simulative error monitoring systems for the evaluation of others’ movements.

Keywords: action observation, error-detection, expert brains, predictive simulation, TMS

Introduction

Achieving musical skills through extensive practice is paralleled by morphofunctional brain changes (Elbert et al. 1995; Schlaug et al. 1995; Pantev et al. 1998; Hund-Georgiadis and von Cramon. 1999; Pascual-Leone 2001; Münüte et al. 2002; Gaser and Schlaug 2003; D’Ausilio et al. 2006; Rosenkranz et al. 2007; Dayan and Cohen 2011). In the domain of musical expertise, motor excellence may be regarded as the ability to detect and reduce movement errors to achieve subtle expressive nuances. Movement errors may occur as failure to achieve the intended goal (e.g., pressing a wrong piano key, high-level errors) or as movements that deviate from the intended ones (e.g., pressing the right piano key with the wrong finger, low-level errors).

High-level and low-level errors seem to be reflected in frontal [anterior cingulate cortex (ACC)] and parietal [parietal cortex (PC)] neural activations, respectively (Desmurget et al. 1999; Krigolson and Holroyd 2006; Krigolson and Holroyd 2007). The sensorimotor system prevents low-level errors by diminishing the discrepancy between the predicted somatosensory consequences of the efferent motor command and the actual somatic and sensory feedback of the executed movement (Sperry 1950; von Holst and Mittelstädt 1950) using “forward” and “inverse” mechanisms (Wolpert and Kawato 1998).

Although audio-motor sensory synchronization and integration is crucial in musical practice (Pantev et al. 1998; D’Ausilio et al. 2006), studies in musicians demonstrate that expert performance may be partly independent from the auditory feedback content (Banton 1995; Finney 1997; Repp 1999). Thus, anticipatory monitoring (Shadmehr et al. 2010) and predictive coding (Wolpert and Kawato 1998) seem fundamental to enable finger movement corrections (Maidhof et al. 2009) before any high-level mistake (i.e., erroneous key pressure) is performed.

During musical execution, pianists choose the fingering of musical phrases that best satisfy their expressive needs according to their individual technique. However, basic scales are learned and rehearsed with coded and fixed standard finger sequences. These basic movements are trained in classical pianists in the early years of practice and induce long-lasting sensorimotor plastic changes that affect motor output (Karni et al. 1995; Parsons et al. 2003; Gentner et al. 2010; Ostry et al. 2010). Thus, standard scale fingering is a good example to study movements in which the correct sequence of key press (i.e., the goal) may be achieved through “incorrect,” nontrained, finger sequence (i.e., low-level error). Here, we sought to determine the role played by anticipatory sensorimotor mechanisms on observation and monitoring of others’ pianistic performance and on error observation.

Importantly, studies demonstrate that the neural mechanisms used to monitor individual task performance and to signal the detection of an error are also activated during observation of others’ errors (Mültner et al. 2004; Van Schie et al. 2004; de Bruijn et al. 2007; Malfait et al. 2010). Connections between the neural mechanisms developed for one’s own and others’ error detection seem to be essential for observational learning (Mattar and Gribble 2005; Brown et al. 2009). Although electroencephalographic markers of error detection hint at a general and supramodal error monitoring system (see Garrido et al. 2009 for review), a possible mechanism for detecting observed errors might be based on the direct sensorimotor coding of the movements. It is thus conceivable that a supramodal error monitoring system is supported by modality-specific sensorimotor-simulative mechanisms.

To test the hypothesis that extensive training may endow the sensorimotor system with the ability to predict expected movements and to rapidly react to the observation of erroneous movements, we recorded the corticospinal excitability of relaxed hand muscles of expert pianists’ while they observed mute clips showing piano fingering errors made by a pianist (the model) (Experiment 1, “somatomotor error detection”). In a second experiment, we tested whether a purely nonmotor, visual training that made musically naïve observers capable of detecting the erroneous performance of the same
pianist of Experiment 1 would be enough to bring about changes in their corticospinal system, contingent upon the observed errors (Experiment 2, “visual error detection”). It is worth noting that the visual training allowed naïve subjects to detect the errors with high accuracy. However, they were not permitted to practice the observed fingering and thus were never provided with somatomotor efferent and afferent feedback concerning the observed errors.

We recorded motor-evoked potential (MEP) amplitudes from 3 hand muscles while expert pianists (Experiment 1) and musically naïve subjects visually trained to recognize fingering errors (Experiment 2) observed correct and incorrect (“low-level” motor errors) fingerings of mute piano scales and then verbally categorized the execution as correct or incorrect. Only 1 of the 3 muscles studied in the observers was used by the model to perform the error (thumb’s abductor pollicis brevis, APB). The other 2 were included as active (i.e., a finger that presses the right key in the correct clips and is replaced by the thumb in the incorrect clips, index’s first dorsal interosseous, FDI) and passive (i.e., a finger that is not directly involved in the error, little finger’s abductor digitii minimi, ADM) control muscles. The excitability of each muscle was tested by delivering single-pulse transcranial magnetic stimulation (TMS) 100, 300, or 700 ms after error onset in different trials (Fig. 1). By combining the neurophysiological data with the individual accuracy in detecting the observed errors, we were able to characterize the impact on corticospinal excitability of error detection.

Thus, we explored in the pianist group any somatotopic and time-selective modulation of the corticospinal excitability for recognized thumb errors with respect to observation of correct executions. Moreover, we explored whether the purely visual fingering error-detection training in naïve non-musicians was sufficient to modulate their corticospinal excitability during their explicit error detection. This approach allowed us to expand the notion of sensory-triggered responses in the motor cortex (Hatsopoulos and Suminski 2011).

Materials and Methods

The experimental procedures were identical in the 2 experiments except for the visual training phase that occurred only in Experiment 2.

Participants

Nine professional pianists (2 females, mean age: 29 years, range: 24–37 years) selected from master courses at the music conservatory of Rome “Santa Cecilia” were recruited for Experiment 1. All pianists practiced around $4 \pm 2$ standard deviation (SD) hours per day at the time of testing and were involved in live performances as well as in teaching activities (they had practiced for $19 \pm 6$ SD years with an age of inception at $10 \pm 5$ SD years). All pianists had bachelor degrees in piano, as well as high school diplomas. Nine musically naïve undergraduate university students (1 male, mean age: 23 years, range: 20–35 years) were recruited for Experiment 2.

Three pianists and 1 naïve subject were left handed as confirmed by the Standard Handedness Inventory (Briggs and Nebes 1975). All the participants had normal or corrected-to-normal visual acuity.

The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out 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 for TMS (Wasserman 1998). Participants gave their written informed consent to take part in the study and received a reimbursement for their participation. No discomfort or adverse effects were reported or noticed in any of the participants.

Visual Stimuli

Black/white clips showed the right hand of a professional pianist performing piano scales from a first-person point of view (see Fig. 1). Clips duration was 2 s (29 frames per clip). Five different piano scales were used (1 C major, 2 different C minor, 2 different D major; correct finger sequence is always 1-2-3-1-2-3-4-5, where 1 = thumb, 2 = index, 3 = middle, 4 = ring finger, and 5 = little finger). The incorrect version of each scale was obtained by asking to the professional pianist to use his thumb to press a key when the correct finger would instead be either the index (1 clip)/middle (4 clips) finger. The fingering error always began after the fourth key press (erroneous finger sequence was 1-2-3-1-2-1-4-5 and 1-2-3-1-1-3-4-5). An image of a static, relaxed hand on the keyboard served as a control stimulus to test baseline corticospinal excitability.

Figure 1. The figure shows the experimental setup with the subject in front of the monitor, the 3 recorded hand muscles (A), examples of correct and incorrect fingerings (B), and a typical trial-event timeline (C).
Electromyography (EMG) and Transcranial Magnetic Stimulation

Surface Ag-AgCl cup electrodes (1-cm-diameter) were placed over the APB, FDI, and ADM of each participant's right hand by using a belly-tendon montage. Recordings were made using a CED Power 1401 (Cambridge Electronic Design Ltd., Cambridge, UK) connected to an Isolated Patient Amplifier System Model D360 (Digitimer Ltd., Hertfordshire, UK), and interfaced with CED Spike 2 software. The second-order Butterworth filter was set between 20 and 2.5 kHz (10 kHz sampling rate). Signals were displayed at a gain of 1000. Auditory feedback of the electromyography (EMG) signals was used to help participants maintain voluntary muscle relaxation during electrophysiological preparation.

Focal TMS was performed with a figure of 8-shaped stimulation coil (outer diameter of each wing 70 mm, Magstim polyurethane-coated coil), connected to a Magstim 200 Mono Pulse (Magstim Whitland, Dyfed, UK), over the left primary motor cortex. The optimal scalp location for eliciting MEPs in all 3 muscles was found by moving the coil in steps of 1 cm until the largest MEP from the less excitable muscle was 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. Individual resting motor threshold (rMT) was defined as the lowest stimulus intensity evoking at least 5 of 10 MEPs with amplitude of at least 50 µV in all muscles. rMT ranged between 31% and 53% of maximum stimulator output (mean ± 1 ± 7% SD) in Experiment 1 and between 38% and 62% (mean 48 ± 13 SD) in Experiment 2. Direct comparison between the TMS rMT of the 2 groups showed a nonsignificant difference (P=0.215) indicating that any between-group differences in the corticospinal modulation induced by error observation could not be explained by nonspecific baseline difference of corticospinal reactivity. Stimulus intensity was kept at 20% above rMT during data collection (mean 50 ± 9% SD in Experiment 1 and 57 ± 15% in Experiment 2). EMG recording started 150 ms before TMS so as to be able to discard trials in which a muscular preactivation (EMG signal exceeding 50 µV) was detected. MEP amplitudes were recorded on a pc and stored for offline analysis.

Procedure

During the experimental sessions, participants were comfortably seated in front of a 17-inch monitor (resolution, 1151 × 964 pixels; refresh frequency, 60 Hz) at a distance of 60 cm with their arms and hands relaxed on a pillow placed on their lap. In Experiment 1, pianists were given one 18-trials practice block (9 correct and 9 incorrect fingerings) during which no TMS was delivered. This procedure allowed subjects to familiarize themselves with the experimental task. In Experiment 2, non-pianist participants were given as many 18-trials practice blocks as they needed to achieve ≥90% accuracy in correctly detecting incorrect fingerings (mean number of blocks 3). Only subjects who achieved these levels of accuracy were tested with TMS. This procedure allowed novices to reach a visual expertise comparable to that of pianists. Participants were tested in 1 session of 9 blocks (6 fingerling blocks, 1 static hand baseline block, and 2 fixation blocks) lasting ∼1 h and a half in total. The order of the 6 fingerling blocks and static block was counterbalanced across participants. Each block consisted of 18 trials (9 correct and 9 incorrect fingerings in the fingerling blocks) with an interstimulus interval of 9 s. The choice of the intertrial interval was based on research by Chen et al. (1997) that showed no change in corticospinal excitability with repetitive TMS at 0.1 Hz for 1 h. Each trial started with a blank black screen lasting 9 s on which a fixation cross appeared for 5 s. The same trial location where the fingerling of the following clip would start. During clip presentation, a single-pulse of TMS, at either 100, 300, or 700 ms from error onset or at matched instants in the correct clips, was delivered while pianists passively watched correct and incorrect fingerings videos (mixed event-related design). Stimulus presentation and randomization were controlled by E-Prime v2.1 software (Psychology Software Tools Inc., Pittsburgh, PA). To study the temporal pattern of modulation of corticospinal excitability in response to fingerling error observation, the magnetic pulse was triggered at 3 different time delays (100, 300, and 700 ms) from error occurrence by a photodiode placed on the screen that sent a TTL signal during the TMS (Fig. 1). The photodiode was triggered by a white dot (not visible to the subjects) placed on the screen on the 3rd, 9th, or 21st posterror onset frame of the clip; each corresponding to 100, 300, and 700 ms after the error was committed. The definition of error onset used in the present study coincides with the first frame of the clip in which a finger unexpectedly starts to move inappropriately and thus breaks the fingerling rule. Importantly, the error is not defined in terms of key press but rather in terms of the initiation of an erroneous movement. The same time intervals were used to trigger the TMS during correct fingerling (CR) clips, static hand observation, and fixation blocks (see Supplementary material for a discussion on neurophysiological responses to the observation of fingerling errors and movement matching). The timing accuracy of the setup was tested before the beginning of the experiment by sending the photodiode TTL signal to the TMS and directly to the EMG device (CED Power 1401, Cambridge Electronic Design Ltd., Cambridge, UK). During the intertrial interval, pianists were asked to verbally code each video as correct or incorrect so as to be able to recode each trial in terms of signal detection [Hit/false alarms (FA)/Miss/correct rejections (CR)], signal = fingerling error; a Hit is the correct detection of the signal, a FA is the detection of the signal when the signal is absent, a Miss is the missed detection of the signal and a CR is the correct detection of missing signal]. By doing so, we were able to exclude from the analyses the trials where the participants actually observed an error but were unable to report it, including in the analyses only trials that were correctly coded as CR executions or errors. Thus, any MEP modulation would be linked to the correct recognition of erroneous/correct trials. At the beginning and at the end of the experimental blocks, 18 MEPs were recorded while subjects fixated a white cross. This measure allowed us to control for TMS effect per se during the experimental procedure.

Data Handling

Individual mean MEP amplitudes were calculated for each experimental condition (18 trials per cell). MEP amplitudes that fell 3 SDs above or below each individual mean for each experimental condition and trials contaminated by muscular preactivation were excluded as outliers and precontracted trials, respectively (4% of total in Experiment 1 and 3% of total in Experiment 2). Mean values of MEP amplitudes of all muscles during Fixation 1 (at the beginning of the experiment) did not differ from Fixation 2 (at the end of the experiment) (all P>0.29) in Experiment 1, thus ruling out the possibility that any modulation found could be due to a reduced excitability of the corticospinal system. In Experiment 2, although ADM MEP amplitudes recorded during Fixation 2 were smaller with respect to those recorded during Fixation 1 (P=0.003, all other P>0.517), this effect did not affect in any way the pattern of results, as ADM did not show any modulation related to the experimental factors. Individual raw MEP values were divided by those recorded during the static hand condition (raw fingerling MEP/raw static hand MEP) to normalize the individual corticospinal excitability to a baseline level. The facilitation of corticospinal excitability associated with movement observation was tested in each experiment by pooling MEPs from all 3 muscles together for each individual and by testing the resulting MEP amplitude against the one measured during static hand observation.

To describe the impact on the overall data variance of type of response, time of stimulation after error onset, and muscle, a 2 (response, CR-Hit) × 5 (time, 100–300–700 ms) × 3 (muscle, ADM-FDI-APB) repeated measures ANOVA was performed on normalized data. This allowed us to study the modulation of the corticospinal excitability related to the detection of fingerling errors (error detection). The significance of the overall analysis was corrected with the Greenhouse and Geisser method. Post hoc comparisons were performed with Tukey test.
Results

Experiment 1

Behavioral

Pianists recognized correct and incorrect fingerings well above chance level (mean overall accuracy 91 ± 5% SD). Mean accuracy in recognizing incorrect fingerings (Hit) was 45 ± 5% SD of total (50%) and correctly recognized videos showing CR was 45 ± 4% SD of total (50%). False alarms (FA) and misses (Miss) rates were 4% ± 3% SD and 4% ± 3% SD respectively (Fig. 2) and were thus not statistically analyzed.

A Hit is defined here as the correct detection of a fingering error, while a correct rejection is the recognition of a correct fingering (error = signal). The decision to consider the error as the signal is based on the notion that the pianists’ sensorimotor system might catch the fingering error based on the prediction of the hand movement, and that the error would represent a deviant signal from the expected one.

On the basis of the behavioral results, we analyzed the modulation of MEP amplitudes by coding the clips according to an explicit error detection criterion (i.e., correct error detections (Hit), correct recognition of CR) which allows highlighting modulations that are linked to the correct recognition of errors and of correct piano fingerings executions.

Neurophysiological

In the pianists group, corticospinal excitability of hand muscles was higher during observation of moving than static hands (P=0.051) (see Experimental Procedures section). For each individual finger, raw MEP amplitudes during movement observation were normalized with respect to MEP amplitudes recorded during observation of a static hand on a keyboard. This procedure allowed us to exclude any interindividual baseline difference from the dataset.

Error Detection

The ANOVA with response (Hit, CR) × time (100, 300, 700 ms) × muscle (APB, FDI, and ADM) showed that Hit trials were associated to higher MEP amplitudes with respect to CR ones (P=0.002, main effect of response, F1,8 = 20.667, GG corrected P=0.002). The interaction between response and time factors (F2,16 = 6.079, GG corrected P=0.019) showed that the facilitation of the corticospinal excitability during Hit trials was absent 100 ms (P=0.999), was clearly significant 300 ms (P=0.002), and was still present as a strong trend 700 ms after error observation (P=0.054) (Fig. 3 right panel). Furthermore, the significant interaction of response and muscle factors (F2,16 = 8.954, GG corrected P=0.013) indicated the facilitation of corticospinal excitability found for Hit trials was restricted to APB (P=0.0004) and did not expand to the other muscles (all Ps>0.973) (Fig. 3 left panel).

To sum up, we found a clear facilitation of the corticospinal excitability when pianists observed fingering errors. This neurophysiological modulation was absent at 100 ms after error observation, it appeared at an early time window (300 ms) and tended to be significant at a longer time interval (700 ms) when pianists detected the error with respect to when they accurately recognized that the fingering was correct. Crucially, the modulation was highly specific for the muscle that would be involved in the execution of the error (APB).

Figure 2. The graph shows the pianists’ and the naïve individuals’ group average ability to, i) recognize incorrect piano fingerings (HIT), ii) recognize correct piano fingerings (correct rejections, CR), iii) erroneously detect errors in correct piano fingerings (false alarms, FA), and iv) erroneously perceive incorrect piano fingerings as correct ones (MISS). Mean ± standard deviation (SD).

Figure 3. The left panel of the figure shows the significant interaction of response and muscle factors where the facilitation of corticospinal excitability found for Hit trials was restricted to APB and did not expand to the other muscles. The right panel of the figure shows the significant interaction between response and time factors in pianists where the facilitation of the corticospinal excitability during Hit trials was absent 100 ms, was clearly significant 300 ms, and was still present as a strong trend 700 ms after error observation. Mean ± standard error mean (SEM).
Experiment 2

Behavioral

Naïve individuals easily reached a level of accuracy in detecting fingering errors comparable to that of the pianists (Acc $t_{(16)} = 0.25$, $P = 0.80$; Hit $t_{(16)} = 0.03$, $P = 0.97$; CR $t_{(16)} = 1.86$, $P = 0.08$; Miss $t_{(16)} = 0.78$, $P = 0.44$; FA $t_{(16)} = -1.74$, $P = 0.10$). Mean overall accuracy of the non-pianists was $91 \pm 4\%$ SD. Mean accuracy in recognizing incorrect fingerings (Hit) was $45 \pm 4\%$ SD of total ($50\%$) and $48 \pm 2\%$ SD of total ($50\%$) in correctly recognizing videos showing correct fingerings (CR). FAs and Miss rates were $2 \pm 2\%$ SD and $5 \pm 4\%$ SD, respectively (Table 1).

Neurophysiological

In the non-pianists group, corticospinal excitability of hand muscles was higher during observation of moving versus static hands ($P = 0.044$), showing the typical pattern of corticospinal reactivity to the observation of hand movements. Thus, any across-group difference during fingerings observation cannot be explained by nonspecific baseline differences. As in Experiment 1, the specific hypothesis of a somatotopic and time-locked modulation of the excitability of the corticospinal system for error detection was investigated performing an ANOVA on MEP amplitudes recorded from 3 muscles of the right hand during the recognition of correct/incorrect fingerings (error detection, CR/Hit trials) at the 3 different time intervals from error onset (100, 300, and 700 ms) (the mean MEP value of each experimental condition is reported in Table 1).

Error Detection

The ANOVA with response (Hit, CR) $\times$ time (100, 300, and 700 ms) $\times$ muscle (APB, FDI, and ADM) showed no main effect or interaction reached statistical significance (all GG corrected $P > 0.157$) except for the response $\times$ time interaction ($F_{2,16} = 4.161$, GG corrected $P = 0.043$). Crucially, however, no comparison between any of the conditions from the response $\times$ time interaction disclosed significant differences (all $P > 0.195$) suggesting that MEP amplitudes were not specifically affected by the response given by naïve individuals at any time from stimulation in this set of stimuli (the mean MEP value of each experimental condition is reported in Table 1).

In sum, after a short-term visual training, naïve subjects were able to detect the fingering errors with an accuracy level comparable to that of expert pianists. However, unlike what found in expert pianists, such perceptual ability was not reflected in a somatotopic-specific modulation of hand’s corticospinal excitability (the graphs showing the nonsignificant response $\times$ muscle interaction and the interaction between response and time are reported as Supplementary material).

These results show that although non-pianists were able to visually detect fingering errors to the same extent as expert pianists, this ability was not paralleled by any correspondent modulation in the excitability of their hand muscles. Crucially, results from the musically naïve group rule out alternative interpretations of what was found in the pianists group. On one hand, the results allow us to exclude that the somatotopic and time-locked facilitation observed in the pianists group might be associated with the fact that, during incorrect fingerings clips, the thumb performed more movements than in the CR clips (see also Supplementary material for further details on this point). Indeed, if the facilitation found in the pianists group had been due to the observation of increased thumb movements, we should have found it also in the non-pianists group. Furthermore, as the level of accuracy in detecting the errors was the same across the 2 groups, the facilitation found in the pianists’ thumb cannot be due to nonspecific perceptual–attentional factors (Kok et al. 2012).

Discussion

The main point of novelty of the present study is that detecting erroneous piano fingering movements induces 1) a somatotopic and 2) a time-locked (i.e., error-locked) facilitation of corticospinal activity in expert pianists. Importantly, although the ability to detect fingering errors was comparable in pianists and musically naïve individuals who were visually trained to achieve high levels of error detection, only the former but not the latter did show a somatotopic corticospinal signature of the recognized errors.

To the best of our knowledge, this is the first report of a somatotopic corticospinal facilitation linked to the observation of erroneous skilled movement. This effect is specific for the muscle controlling the finger that performs the error in the observed fingering, and it does not extend to hand muscles not involved in the fingering error (FDI and ADM). Furthermore, pianists show a nonsomatotopic modulation associated to error detection, which is time-locked to the error, and takes the form of a significant increase of excitability 300 and 700 ms, but not 100 ms, after its observation.

Such timing is consistent with studies showing enhanced late Pe (error positivity, 400–600 ms) amplitude over the parietal cortex when subjects perceive an error in their own performance. These results show that higher sensorimotor activations for detection of others’ error in sensorimotor expert observers are time and muscle specific.

Table 1

Mean MEP amplitudes of all experimental conditions for naïve participants in Experiment 2 (values represent the amplitude of raw MEPs recorded during clip observation divided by individual raw MEP amplitude recorded during static hand observation)

<table>
<thead>
<tr>
<th>Time (ms)</th>
<th>Muscle</th>
<th>Accurate</th>
<th>Inaccurate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Correct</td>
<td>Correct</td>
</tr>
<tr>
<td>ADM</td>
<td></td>
<td>1.42 ± 0.20</td>
<td>1.43 ± 0.23</td>
</tr>
<tr>
<td>FDI</td>
<td></td>
<td>1.16 ± 0.06</td>
<td>1.11 ± 0.06</td>
</tr>
<tr>
<td>APB</td>
<td></td>
<td>1.62 ± 0.36</td>
<td>1.49 ± 0.25</td>
</tr>
<tr>
<td>ADM</td>
<td></td>
<td>1.41 ± 0.19</td>
<td>1.45 ± 0.19</td>
</tr>
<tr>
<td>FDI</td>
<td></td>
<td>1.14 ± 0.05</td>
<td>1.16 ± 0.06</td>
</tr>
<tr>
<td>APB</td>
<td></td>
<td>1.50 ± 0.32</td>
<td>1.78 ± 0.33</td>
</tr>
<tr>
<td>ADM</td>
<td></td>
<td>1.56 ± 0.21</td>
<td>1.64 ± 0.21</td>
</tr>
<tr>
<td>FDI</td>
<td></td>
<td>1.16 ± 0.06</td>
<td>1.09 ± 0.06</td>
</tr>
<tr>
<td>APB</td>
<td></td>
<td>1.46 ± 0.24</td>
<td>1.45 ± 0.28</td>
</tr>
</tbody>
</table>

Mean ± SEM.
Given the present correlational approach, it is not possible to distinguish whether the reported facilitation is a reflection of early “supramodal” error-related activity (error-related negativity/error positivity, ERN/Pe, or mismatch negativity) generated by a general error-detection system in the ACC or, if, conversely, it represents an early somatotopic-specific marker of the error that precedes any ACC activity.

**Expert Pianists Show Anticipatory Somatomotor Signatures of Others’ Errors Detection**

Although a link between the neural substrates of monitoring one’s own and others’ errors has already been reported (Miltner et al. 2004; Van Schie et al. 2004), here we demonstrate for the first time that the mismatch between the observed erroneous movement and the correct predicted one induces a selective enhancement of the excitability of the same muscle that would perform the observed error. The evidence that musically naïve individuals did not show such modulation highlights that visual training in detecting the finging error is not sufficient in inducing any somatotopic corticospinal facilitation.

Extensive motor training modifies the output signal sent by the primary motor cortex to the corticospinal tract (Classen et al. 1998) and also changes the organization of the cortico-muscular system (Gentner et al. 2010). Studies indicate that sensorimotor training endows the brain with perceptual monitoring mechanisms (Rabbitt 1978) that may be further tuned by predictive action simulation (Knoblich and Flach 2001; Wilson and Knoblich 2005; Aglioti et al. 2008). Importantly, in musical performance, the control of actual movements is anticipatory in nature as sensory feedback is time-delayed and too slow to correct fast finger movements. Here, we provide evidence that in experts, neurophysiological reactions to error detection are based on anticipatory simulative-like mechanisms. Indeed, during actual movement execution, error detection (and motor correction) is thought to rely on the mismatch generated by the availability of anticipatory motor efferent copies, which are sent from the premotor cortex to the somatosensory parietal system via corollary discharges (Christensen et al. 2007), and the actual sensory feedback. In the present case, passive observation of fingering may be sufficient to trigger anticipatory simulative-like mechanisms in expert pianists that allow them to monitor the accuracy of the movement. Thus, the MEP modulation may represent the corticospinal reflection of the mismatch originating from the discrepancy between expected and observed movements. Interestingly, this mismatch can only be detected if the observer had previously created a strong and refined sensorimotor prediction of the expected movements from the experience of direct motor practice.

A recent behavioral and fMRI study demonstrated that audio–visual binding is stronger in pianists versus non-pianists when listening to music but not to speech (Lee and Noppeney 2011). This result indicates that somatosensory and motor expertise in piano playing finely tunes an internal forward model that provides precise and specific predictions—crucial for execution—about the relative timings of auditory and visual signals (Lee and Noppeney 2011). Our data complement and significantly extend previous knowledge by providing direct evidence of a corticospinal modulation suggesting that fast and detailed motor predictions are triggered by piano fingering observation in sensorimotor experts. This evidence is coherent with the notion that motor prediction, which likely originates in premotor-supplementary motor regions, takes into account somatotopy as a fundamental rule used for action execution (Urgesi et al. 2006; Urgesi et al. 2010; Avenanti et al. 2012).

**Facilitation of Corticospinal Excitability for Observed Errors**

We provide the first evidence of time-specific somatotopic corticospinal facilitation for erroneous movement observation by showing that the excitation of the motor system is affected by error observation only in the finger that commits the error and only 300 and 700 ms after error onset but not at earlier time-window (100 ms). Corticospinal facilitation has been found during the observation of biomechanically possible (Fadiga et al. 1995) and impossible movements (Romani et al. 2005; Avenanti et al. 2007), mental motor imagery (Fourkas et al. 2006; Bufalari et al. 2010), and during passive observation of static body postures that imply an action (Urgesi et al. 2006; Candidi et al. 2010; Urgesi et al. 2010). Here, we show that observing piano fingerings that violate the experience-based matching between the motor copy of over trained movements and their observed counterparts induces an increase in corticospinal reactivity, as though specific somatotomotor mechanisms monitor the discrepancy between expected and observed actions. Physiological data coherent with forward models of action control suggest that the motor system reduces sensory feedbacks of performed actions by sending filtering, cerebello-cortical (Miall 1998) and premotor-cortical (Christensen et al. 2007), corollary discharges to the somatosensory system. Importantly, the sensory suppression exerted by these corollary discharges during movement execution originates from central signals related to the preparation of movements (i.e., these corollary discharges are anticipatory) and occurs upstream the primary motor cortex (Voss et al. 2006). Thus, expected sensory feedbacks are known to engender a reduced neural response with respect to unexpected ones both in the auditory (Heinks-Maldonado et al. 2005) and in the sensorimotor (Blakemore et al. 1999) domains. Conversely, unexpected somatosensory feedback, induced by passive muscle vibration, generate enhanced motor reactivity (Rosenkranz et al. 2003) and greater sensory experience (Blakemore et al. 2000). Our results suggest that the pianists’ sensorimotor system activates an anticipatory motor simulation of the observed fingering movements (Umiltà et al. 2001; Urgesi et al. 2010), thus providing the nervous system with a “filtering prediction” of what should be observed. The facilitation we found in expert pianists when observing fingering errors might be originated by the inefficacy of the predicted motor simulation to reduce the unexpected visual inflow. One of the core advantages of a correspondence between the neural mechanisms developed for one’s own and others’ error detection is that movement errors are not only important for action execution but also for learning by watching (Mattar and Gribble 2005). Thus, the reported MEPs facilitation during observation of incorrect fingerings may represent the critical signal for observational learning. This is in accordance with the interference on observational action learning induced by inactivation of the primary motor cortex (Brown et al. 2009).
Timing of Modulation Induced by Error Detection

The pattern of results we found show that the corticospinal signature of detected error is reflected in the motor system 300 ms after observed error onset at the earliest and remains evident 700 ms later.

Although speculatively, we suggest that this pattern of results is concordant with error-related electroencephalographic data. Indeed, the earliest electroencephalographic activity related to one’s own error monitoring is recorded within the first 70–100 ms after error occurrence [ERN (Falkenstein et al. 1991; Falkenstein et al. 2000)] and is thought to be unrelated to error awareness (Nieuwenhuis et al. 2001; Endrass et al. 2007; O’Connell et al. 2007; Pavone et al. 2009). This early brain potential is followed by a long, positive potential (Pe) which comprises 2 subcomponents: an early Pe (200–300 ms) that is thought not to be affected by error awareness and a later Pe (400–600 ms) which seems to be a marker of error awareness (Van Veen and Carter 2002; Herrmann et al. 2004; Overbeek et al. 2005; Endrass et al. 2007).

Relevant to our study is that brain potentials evoked by observation of others’ errors show a delayed latency of about 150–200 ms with respect to the errors committed in first-person (Milner et al. 2004; Van Schie et al. 2004). The latency of the corticospinal modulation found in our expert pianists is thus consistent with the timing of early error-detection-related brain potentials (ERN 100 ms, Pe 200–300 ms) although it is not possible to exclude that early (300 ms) and late (700 ms) modulations may reflected different cognitive processes. Although the present data do not allow any specific interpretation of the functional difference between early and late facilitation, it is entirely plausible that the late activity may have different neural underpinnings and different functional meaning from the earlier activity (e.g., it may index the attempt to correct the erroneous movement).

Visual Detection of Observed Errors

Although able to detect the fingering errors after a pure visual training, musically naïve subjects did not show corticospinal signatures of error detection. Importantly, a general increase of MEPs to action observation was found also in these subjects indicating their lack of sensitivity to errors is not explained by defective corticospinal reactivity during piano fingering movements. Thus, developing a mere visual strategy for spotting the errors does not imply a predictive somatomotor simulation of the observed movements and error detection. The present data seem to suggest that, in the absence of motoric expertise, subjects may likely detect the errors relying more on reactive rather than predictive mechanisms. Studies have shown that the direct personal somatomotor experience is crucial for mapping the observed actions onto the observers’ sensorimotor system (Calvo-Merino et al. 2005, 2006). Importantly, the analysis of corticospinal reactivity during observation of basketball free throws shows that somatomotor action mapping seems to be inherently anticipatory in visuomotor experts but not in visual experts (Aglioti et al. 2008). Our results advance previous knowledge by showing that although detection of errors may occur at purely perceptual level, somatomotor simulation is sensitive to a predictive coding of errors in expert musicians who observe domain-specific movements, and it correlates with error coding in somatotopic and time-locked terms.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

Funding

S.M.A. is funded by the Istituto Italiano di Tecnologia SEED 2009 (Protocol Number 21538), by grants from the Ministero Istruzione Universita’ e Ricerca (Progetti di Ricerca di Interesse Nazionale, PRIN 2009) and by the European FP7 Grant Tango. The project Tango acknowledges the financial support of the Future and Emerging Technologies (FET) program within the Seventh Framework Programme for Research of the European Commission, under FET-Open Grant number 249858. MC is funded by Sapienza Progetti di Ricerca 2011 (Protocol Number C26A115CM5).

Notes

We thank Dr Emiliano Pes for providing the stimuli used in the study and Dr Pietro Fermani for technical advice. M.C. designed research, performed research, analyzed data, and wrote the paper; L.M.S. performed research, analyzed data, and wrote the paper; L.M. performed research; S.M.A. designed research and wrote the paper. Conflict of Interest: None declared.

References


