Dominance of Vision over Proprioception on Motor Programming: Evidence from ERP

The brain determines positions and movements of body parts from inputs arising at least from vision and proprioception. Using the brain event-related potential called the lateralized readiness potential, which reflects motor cortical activity during motor programming, we showed in a motor task that viewing one hand in a sagittal mirror—giving the impression to see the opposite hand—generated activity in the motor cortex of the seen hand (i.e., of the nonmoving hand hidden behind the mirror). The visual influence on cortical motor region occurred even when the proprioceptive input related to the real opposite effector was not aligned on the visual feedback of the hand given by the mirror. This dominance vision over proprioception was greatly reduced when the task was executed in the dark with hand position represented by small lights fixed on the moving hand, with no motor activity being recorded in the cortical area of the inactive hand. These results give new insights into how the brain weights and integrates visual and proprioceptive information in motor control.

Keywords: LRP, mirror paradigm, motor control, perception

Introduction
The brain determines the position and movements of the hand from inputs from at least 2 senses: vision (the viewed position of the hand initially in an eye-centered reference frame) and proprioception (the felt position of the hand via muscle and joint receptors). Interactions between these 2 sensory inputs have been described in experiments inducing conflicts between vision and proprioception (Hay et al. 1965; Rossetti et al. 1993; Berberovic and Mattingley 2003; Michel et al. 2003a, 2003b) and in experiments with sensory-deficit patients, such as deafferented subjects and amputees (Lajoie et al. 1992; Nico et al. 2004; Stenneken et al. 2006a, 2006b).

It has been shown in healthy subjects that combined visual and proprioceptive information (when both are available) improves the performance of hand localization tasks relative to an unimodal condition of only vision or proprioception (van Beers et al. 1999). The weighting given to vision and proprioception in the central nervous system is still debated, but it has often been proposed that estimating the hand position relies more on vision than on proprioception (Hay et al. 1965; Rossetti et al. 1995; Mon-Williams et al. 1997). Indeed, incorrect visual feedback on the position of one hand, such as induced using prism spectacles, has been shown to bias the feeling of where that hand is in space. Prisms disrupt the usual congruence between proprioceptive and visual information by deviating the visual field unilaterally. However, it has also been shown that the role of proprioception in hand localization increases in a degraded viewing environment, such as when the task is completed in darkness with the limb position indicated only by a light-emitting diode (LED) taped to the finger (Mon-Williams et al. 1997). Vision and proprioception participate also in motor control and in guiding limb movements. Thus, using prisms to change the visual input leads also to reaching and pointing errors due to misperception of the location of visual targets relative to the limb (Rosetti et al. 1995). Motor control has also been shown to be affected by incongruent visuo-proprioceptive inputs produced by a frontal mirror (Lajoie et al. 1992). Interestingly, differences have been noted in the behaviors of a deafferented patient without proprioception and normal controls in a mirror-based drawing task in which subjects had to trace a 6-pointed star pattern as fast and accurately as possible while viewing the image of the drawing hand in a frontal mirror. Under this condition, Lajoie et al. (1992) showed that healthy subjects required several trials to attain the performance of a patient suffering a total loss of proprioception. For normal subjects, the inversion of visual coordinates induced by the mirror produced the need for a visual recalibration of proprioception, whereas it appeared to be a simple visual tracking task to the deafferented patient. Fascinating clinical observations in upper limb amputees have also been reported by Ramachandran and Rogers-Ramachandran (1996). In their studies, a mirror was oriented in the midsagittal plane of traumatic amputees with the reflective surface facing the intact limb. In that scenario, the hand in the mirror occupied the place of the amputated hand. Some patients described vivid kinesthetic sensations in the missing hand when movements of the valid one were visually superimposed at the place of the missing hand using a lateral mirror. These observations have led to use the mirror as a therapeutic tool that has shown efficiency in accelerating recovery of function from a wide range of neurological disorders such as phantom pain and peripheral nerve injury (see Ramachandran and Altschuler 2009 for a review). It has been shown in normally limbed subjects that illusions of ownership of a hand seen in a mirror are not required to bias proprioception (Holmes et al. 2006) and even that a discrepancy between proprioception and vision of the body, enabled by the means of 2 mirrors, allows one to feel as if he is standing outside himself (Altschuler and Ramachandran 2007). These observations question the extent to which the felt position of a body part is influenced by visual input. Holmes et al. (2004, 2006) addressed this question by manipulating the position of the right hand hidden behind a mirror while controlling visual cues concerning either its position or appearance using a lateral mirror reflection of the real hand, a rubber hand, or a wooden block. The results indicated that the visual cue strongly affected the reaching performance: A proprioceptive bias was
evident not only when the apparent position of the hand in the mirror and the actual position of the hidden hand were incongruent but also when a rubber hand was viewed in the mirror. The reaching bias recorded when viewing a wooden block was significantly smaller than in hand and rubber hand conditions, indicating the importance of vision itself and the features of the available visual information. These results confirm that reaching movements are guided by a combination of visual and proprioceptive cues and highlight the role that vision may play as a kinesthetic surrogate in the human sensory system. In the mirror situation, visual cues may have influenced the representation of the arm position. Pointing and reaching errors in the mirror and prism paradigms provide a behavioral measure of variations of proprioceptions weighting relative to that of vision, but there is little physiological evidence of this phenomenon. Anatomically, some areas of convergence of visual and proprioceptive information have been localized in both animal and human brains (Graziano 1999; Ehrsson et al. 2004). Neurophysiological studies using functional magnetic resonance imaging (fMRI) in healthy humans have associated activity in the premotor cortex with the feeling of ownership of a seen limb (Ehrsson et al. 2004) and have localized right temporoparietal cortex activation during visuopropiopceptive conflict (Balslev et al. 2005). More importantly, activation of the primary motor cortex (MI) has been observed during the proprioceptive perception of limb movement, even if the limb itself is not moving (Naito et al. 2002). The aim of the present study is to determine if this motor cortical activation can be shown when the perception of limb movement is given by vision.

If the motor areas receive visual and proprioceptive information to match tight temporal constraints of visuomotor control when executing a voluntary movement, and if vision plays a dominant role over the representation of the arm position, it could be hypothesized that the image of one hand that will execute a movement would lead to cortical motor programming related to the viewed hand, even if the real one will not move. We tested this hypothesis using experiments in which subjects performed movements with their right hand, which could only be seen in a sagittal mirror, thereby giving the impression that the left hand was performing the task. The hidden real left hand was in either a congruent or a completely incongruent position with respect to the viewed hand in the mirror. Activation of motor cortices related to the active and observed hands was assessed by analyzing the brain event-related potential (ERP) called the lateralized readiness potential (LRP), which reflects only movement-related parameters and effectively isolates activities that reflect only lateralized response preparation. More importantly, neuroanatomical data from surface- and deep-electrode recordings have shown that the LRP is at least partly generated in the MI (Vaughan et al. 1968; Okada et al. 1982; Gambra et al. 1990). In addition, the LRP component reflects response preparation and commences before muscle contraction begins and therefore can occur in the absence of an overt response (de Jong et al. 1988; Miller and Hackley 1992; Galdo-Alvarez and Carrillo-de-la-Pena 2004; Minelli et al. 2007).

We hypothesized that observing movements of one’s own hand in a mirror, giving the impression of movements of the opposite, nonmoving hand, will generate an LRP in relation to activations in the cortical motor regions of the nonmoving hands independently of its position (proprioceptive information). The critical observation is whether LRPs are observed or not under lateral visual feedback condition.

Experiment 1

Experiment 1 investigated whether the view of a left hand executing an action induces motor preparatory activity in the right motor cortex. We examined the influence of viewing the reflection of the right hand in a sagittal mirror (giving the impression of seeing the left hand), while the real left hand was in either a congruent or an incongruent position related to the image of the reflected hand in the mirror.

Materials and Methods

Participants

Eight healthy paid volunteers (2 males, 6 females; mean age 32.2 years) were enrolled in the experiment. Seven of the participants reported that they were right-handed. The experiment was approved by the local ethics committee, and the subjects gave their informed consent prior to participation.

Procedures

Subjects performed a forced-choice task unimanually under 6 different and randomly presented conditions, defined by different views of the responding hand and positions of the inactive hand. Participants were seated at a table in the experimental room. Depending on the experimental condition, a mirror was placed either vertically (in the middle of the table on the midsagittal plane of the subject with the reflective surface facing the right arm) or frontally (with the reflective surface facing the subject’s right hand) or was absent (no-mirror condition). Two LEDs were placed on the table 3 cm apart, 50 cm from the subject, and on the side of the responding hand, with 2 response keys placed beside the LEDs (Fig. 1). Subjects were instructed to maintain eye fixation between the 2 target lights. The LEDs were switched on randomly for 200 ms, and subjects were asked to press—as quickly as possible—the upper (lower) button when the upper (lower) LED was switched on under the following 6 conditions:

1. Participants had a direct view of the right (performing) hand (no-mirror condition).
2. The task was performed using the left hand as per condition 1 (i.e., with a direct view of the performing hand, corresponding to the no-mirror condition).
3. Subjects performed the task with the right hand with the sagittal mirror, which gave the impression of a direct view of the left (inactive) hand. The real left hand was placed on the table symmetrically to the responding hand (in congruence with the image in the mirror).
4. Similar to condition 3, but participants kept their left hand closed (fist) behind the mirror (in an incongruent position compared with the image in the mirror).
5. Similar to condition 3, but the left arm was positioned behind the back of the subject (in an incongruent position).
6. The mirror was placed frontally, giving visual feedback on the right hand in a frontal view.

An opaque cover was used to prevent direct vision of the right performing hand in all conditions involving a mirror (conditions 3–6). One hundred and thirty trials randomly
Electrophysiological recordings. Electroencephalographs (EEGs) were recorded using Ag/AgCl active electrodes (Biosemi B.V., Amsterdam, The Netherlands) mounted in an elastic cap. The electrodes were placed at sites C3 and C4 according to the 10-20 system (Klem et al. 1999) above the hand area of the left and right motor cortices and sampled at 512 Hz (bandpass filtered from 0.02 to 100 Hz, with off-line digital smoothing with a 10-Hz cutoff). To monitor ocular artifacts, vertical electrooculographic (VEOG) potentials were recorded from bipolar derivations using Ag/AgCl electrodes placed above and below the right eye and filtered with the same parameters as the EEG data. These artifacts related to the task and could reflect either eye blinks or visual displacement to the hand or target lights. Horizontal electrooculographic potentials were not recorded because 1) no lateral distractor was present and 2) VEOG derivations were sensitive enough to detect horizontal eye movements. The muscle activity of both hands was recorded by electromyography (EMG) using bipolar derivations placed at sites on the ventral forearm that roughly trisected the wrist–elbow distance and bandpass filtered from 0.3 to 500 Hz.

Ocular, cerebral, and muscular artifact rejection and the duration of the averaging epoch ranged from 200 ms before stimulus onset to 500 ms after stimulus onset. Segments containing any eye movements or muscular movements from the nonperforming hand were excluded from the analysis. After rejecting invalid trials, data analyses were performed on a mean of 119.5 trials per condition and subject.

EEG analysis. To calculate response-specific lateralization according to the viewed hand, ERPs were computed separately for each of the 6 conditions defined by the visual feedback of the performing hand and were subjected to the following 2-step subtraction procedure that accounted for unilateral motor activity evoked by voluntary movements: (1) the difference in waveforms between sites C3 and C4 was calculated for each trial and condition and (2) the averaged waveform for trials under conditions 2-5 was subtracted from the averaged waveform for trials under condition 1, leading to 5 different waveforms. This analysis meant that a comparison of conditions 1 and 2 should measure the classic LRP (i.e., response preparation/execution for either the left or right hand) and can be written as

\[ \text{LRP} = (C3 - C4)_{\text{right hand (condition 1)}} - (C3 - C4)_{\text{left hand (condition 2)}}. \]

Comparison of conditions 1 and 3 should measure the LRP due to hand vision in the lateral mirror in the congruent visuoproprioceptive condition; comparison of conditions 1 and 4 should measure the LRP due to hand vision in the lateral mirror in the presence of weak visuoproprioceptive incongruency (only the posture of the left and viewed hands differed), and comparison of conditions 1 and 5 should measure the LRP due to hand vision in the lateral mirror in the presence of strong visuoproprioceptive incongruency (spatial positions differing between the left and viewed hands). Conditions 1 and 6 were also compared as a control waveform, in which no LRP was expected. Indeed, subtracting a negative waveform induced by the movement of the right hand (condition 1) from a similar negative waveform induced by the movement of the right hand seen in the frontal mirror (condition 6) should result in a baseline waveform, and this was termed the control potential.

Electrophysiological Results

Analysis of presubtracted and lateralized waveforms recorded by electrodes at sites C3 and C4 has been shown to be redundant (Miller and Hackley 1992). Consequently, we performed statistical analyses only on LRPs. The 5 waveforms from the 6 conditions are illustrated in Figure 2. ERP amplitudes were analyzed for 200 ms following LRP onset. The onset of LRP was estimated for each subject using a segmented regression method, based on averaged ERPs (Mordkoff and Gianaros 2000). In this method, the LRP onset was defined as the point of intersection between 2 straight lines fitted to the LRP waveform: one line fitted to the putative preonset segment of the LRP and the other fitted to the segment that rose to the peak. Right and left hand movements under direct view conditions yielded an LRP...
Figure 2. (A–E) The 5 grand averaged waveforms and standard error of the mean ($N = 8$) from the 6 experimental conditions defined by the visual feedback on the performing hand in experiment 1 and their corresponding EMG (right and left hand) and EOG activity. Negative is plotted upward.
In addition, and as anticipated, LRs were observed when electrophysiological activity under lateral mirror view conditions—giving the impression that the left hand was performing the task—were subtracted from activity under direct view conditions (condition 1 vs. condition 3, condition 1 vs. condition 4, and condition 1 vs. condition 5). This observation indicates that activation of the left hand motor areas (right hemisphere) was associated with a right hand response that was independent of the position of the hidden real left hand. Unexpectedly, a small lateralized potential was also present with a frontal view of the moving hand (control potential: condition 1 vs. condition 6), suggesting activity in the right hemisphere, although it was significantly lower than the classic and lateral mirror-induced LRs.

Inspections of waveforms (C3–C4) before the subtraction of conditions confirmed the hypothesis that activation of the left hand cortical motor areas (right hemisphere) was associated with a right hand response when viewed in the sagittally placed mirror. Figure 3B–D (gray lines) show that performance of a right hand movement under lateral mirror conditions (giving the impression that the left hand is performing the task) generates a signal that resembles the signal recorded when the left hand is performing the task (Fig. 3A gray line). However, the effect of the right hand motor execution on the left cortical motor area is not abolished under lateral mirror conditions. Hence, a small negativity preceding the movement is observed over the contralateral hemisphere of the right hand under lateral mirror conditions; this would be expected because M1 is an output motor area, and a right hand movement has been executed. Figure 3E indicates that the negativity observed in the control potential (condition 1 vs. condition 6), which is more than a motor lateralization (ipsilateral enhancement), may be due to a modulation of the contralateral motor activity of M1 owing to the frontal visual feedback of the right hand.

This negative signal (related to the control potential, see Fig. 2E) was not clearly visible for each subject, so the mean amplitude of the control potential waveform was computed for 200 ms after the mean latency between the LRP and the 3 LRs induced by the mirror (which was 205 ms). The control potential differed significantly from the 0 baseline, $t = -4.89$, $P = 0.002$. Analysis of variance (ANOVA) showed a significant difference in amplitudes ($F_{4,28} = 14.31$, $P < 0.001$, Fig. 2), and the post hoc Newman–Keuls test showed a significant difference between all LRs (classic LRP and the 3 lateral mirror–induced LRs) and the control potential ($P < 0.05$), whereas amplitudes of the classic and lateral mirror–induced LRs did not.

**Figure 3.** (C3–C4) values for each condition before the subtraction procedure. (A) Classic LRs, (B) LRs induced by the sagittally placed mirror, (C) LRs induced by the sagittally placed mirror when the left hand is closed behind the mirror, (D) LRs induced by the sagittally placed mirror when the left hand is behind the subject, and (E) LRs for the control potential when the mirror is placed frontally.
not differ significantly. Importantly, in the lateral mirror conditions, even when the EEG deflection was observed in the hemisphere contralateral to the viewed hand, EMG records indicated that no actual movements were executed by this hand (i.e., the left hand placed behind the mirror, Fig. 2B–E, EMG left hand). An ANOVA on EMG data indicates no difference between the amplitude at the baseline amplitude (defined by 200 ms preceding LRP onset for each of the 4 conditions) and the EMG amplitude recorded from the LRP onset to the subsequent 200 ms ($F_{1,7} = 3.87, P = 0.09$).

In addition, it has to be noticed that different amplitudes are observed between the right hand cortical response and the left hand cortical response (Fig. 3A, black line and gray line, respectively). This difference is significant and is most likely due to the fact that almost all the participants of the study were right-handed (7/8). Hence, the mean cortical response generated by a right hand movement could therefore be more important than the mean cortical response generated by a left hand movement.

**Latency Measures**

A repeated-measures analysis revealed a significant difference between onsets of the 4 LRPs. The classic LRP began at a mean of 145 ms following stimulus onset. This latency was shorter than that for all 3 LRPs induced by the lateral mirror view (246 ms for the LRP induced by the lateral mirror, 208 ms for the LRP with left hand fist, 221 ms for the LRP with left hand in the back, $P < 0.05$ for the 3 post hoc comparisons, Newman–Keuls test). Inspection of the (C3–C4) curves plotted in Figure 3B–D shows that in conditions 3, 4, and 5 (gray lines) the initial response is in the direction expected from a motor output signal (of the actually moving hand) to decrease only after 250 ms. This explains the longer latency of the LRP for these conditions.

**Behavioral Results**

Average reaction times (RTs) for each condition are shown in Tables 1. Although RTs differed significantly among conditions ($F_{4,28} = 4.5, P = 0.006$), significant differences were only observed between conditions 1 (direct view of the right hand) and 6 (frontal mirror view) and between conditions 4 (lateral mirror view with the left hand close behind the mirror) and 6 ($P = 0.004$ and $P = 0.03$, respectively, Newman–Keuls test). These differences may reflect levels of difficulty linked to the spatial uncertainty of the positions of the response keys under mirror conditions, with the easiest condition being condition 1 (direct view of the right hand, mean = 649 ms) and most difficult being condition 6 (frontal mirror view, mean = 760 ms). All other comparisons were not significant, but a trend in increased RT was observed for almost all other conditions when compared with the direct view condition. However, care should be taken in drawing conclusions about the absence of differences among conditions because only 8 subjects participated in the present experiment, yielding low statistical power.

**Discussion**

The results of experiment 1 indicate that vision of an image of one’s own hand is sufficient to generate cortical activity related to that hand, even if the opposite hand actually performs the movement. Furthermore, we observed a lateralized motor activation even when the proprioceptive information of the hidden hand was not aligned with the visual information of the image of the hand in the lateral mirror. Indeed, when the real left hand was positioned behind the participant’s back, the vision of that hand in a proprioceptively possible (but different) position generated activity in the right hemisphere. The sole difference between the classic LRP and the sagittal mirror-induced LRPs was in term of latency, explained by the fact that the sagittal mirror conditions generated first a cortical motor activity in the direction expected from a motor output signal (emerging in the left hemisphere) before changing direction (in the right hemisphere). Moreover, the reversion of the potential occurred before any visual information of movement was available, indicating not only that a motor potential was recorded in absence of an overt movement (de Jong et al. 1988; Miller and Hackley 1992; Galdo-Alvarez and Carrillo-de-la-Pena 2004; Minelli et al. 2007) but also that the brain can make predictions of expected sensory consequences of actions (Blakemore et al. 2002), even in the mirror condition. Forward models have been proposed to explain the causal relationship between actions and their sensory consequences by using an efference copy of the motor command to make a prediction of the sensory consequences of the movement. Thus, in the present study, a motor activation related to the visual feedback of the hand could reflect a process aimed to reduce the discrepancy resulting form the comparison between the predicted and actual sensory feedback.

Frontal viewing of the right hand—even though it appears as a left hand—did not generate a motor activity in the right hemisphere. In the frontal and sagittal mirror conditions, the positions of the hidden real left hand and the viewed left hand (either in the frontal or sagittal mirror) were congruent. The clear presence of an LRP for the sagittal mirror but not for the frontal mirror might be due to coherence of the visual information of a left hand in an anatomically plausible position, even if the real left hand is not in that position: The viewed hand is in a proprioceptively possible position in the lateral condition but not in the frontal condition. Postural information relating to the hidden left hand does not appear to interfere with motor activity that reflects the LRP. This is confirmed by the similarity of the LRPs in the visuoprooprioceptive congruent and incongruent conditions, that is, motor activity appeared to be independent of the position of the inactive hand. This observation underlines the strength of the visual feature of the stimulus and questioned the extent to which the motor activity

---

**Table 1**

Behavioral results—experiment 1: mean RTs in milliseconds (standard deviation)

<table>
<thead>
<tr>
<th>Condition</th>
<th>Direct view of the right hand (condition 1)</th>
<th>Lateral mirror view in visuoprooprioceptive congruence (condition 3)</th>
<th>Lateral mirror view in visuoprooprioceptive incongruence (condition 4)</th>
<th>Lateral mirror view in strong visuoprooprioceptive incongruence (condition 5)</th>
<th>Frontal mirror view (condition 6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RT (ms)</td>
<td>649 (85 ms)</td>
<td>717 (120 ms)</td>
<td>677 (117 ms)</td>
<td>715 (119 ms)</td>
<td>760 (83 ms)</td>
</tr>
</tbody>
</table>
related to the hidden hand following a lateral mirror view is exclusively based on visual information about the hand position. In order to determine whether the visual information about the hand is mandatory to record an LRP in the sagittal mirror condition, a second experiment was conducted. A way to give a feedback of hand position without relying on visual input is to reduce the intensity or resolution of visual information of the hand. Providing an incomplete visual information of the hand (induced by using only LEDs on the hand in darkness) will allow to determine if visual features stimuli (hand) are necessary to obtain an LRP, that is, the activation of motor cortical areas through visual inputs of the hand.

### Experiment 2

We conducted a second experiment to determine whether vision of the hand is crucial to generate a motor activity of a seen limb. Based on previous experimental findings (Mon-Williams et al. 1997; Plooy et al. 1998) that have shown that in a sparse visual environment visual dominance over proprioception decreases, we hypothesized that the privation of acute visual information about the hand would reduce the visual influence on motor regions. As a consequence, a poor visual information of the active hand through the lateral mirror would not be enough to elicit motor activity in the controlateral hemisphere, and no LRP would be expected. Information about the hand position and movement was restituted by the means of LEDs fixed on the hand in darkness (induced by using only LEDs on the hand in darkness) will allow to determine if visual features stimuli (hand) are necessary to obtain an LRP, that is, the activation of motor cortical areas through visual inputs of the hand.

### Materials and Methods

Experiment 2 was completed in total darkness and was identical to experiment 1 except as described below.

#### Participants

Ten healthy paid volunteers (5 males, 5 females; mean age = 26.6 years) were enrolled in experiment 2. Nine of the participants reported that they were right-handed, 5 of whom had participated in experiment 1.

#### Procedures

Visual information of the participant’s performing hand was provided by 16 LEDs fixed to a black glove worn on the hand (3 LEDs per finger plus 1 on the back of the hand). The task in experiment 2 was performed under the following 4 randomly presented conditions defined by different views of the LEDs on the responding hands:

1. Participants performed the task with their right hand while receiving direct visual feedback on the position of this hand from the LEDs.
2. The task was performed using the left hand as per condition 1.
3. Subjects performed the task with the right hand with a sagittal mirror. The LEDs on the performing hand viewed in the mirror appeared to be at the position of the left hand.
4. The mirror was placed frontally, giving visual feedback on the positions of the LEDs in a frontal view.

In experiment 1, lateral mirror–induced LRPs did not differ in amplitude or latency, and no LRP was expected in the darkness in the lateral mirror condition; therefore, this experiment did not include left hand close and left hand in participants back conditions. Before each condition, subjects actively moved their hand for 2 min while viewing the LEDs on the glove in order to enhance the representation of their hand in the dark.

One hundred and thirty trials randomly spaced from 2600 to 3000 ms were performed under each condition. Subjects had to perform the same task as in experiment 1.

#### EEG recording

The recording method was the same as in experiment 1 except that data analyses were performed on a mean of 113.5 trials after artifact rejections. This mean did not differ significantly from the mean number of trials in experiment 1 (119.5). $F_{4,13} = 0.89, P > 0.05$. Consequently, the number of artifact rejections was similar in both experiments.

### Electrophysiological Results

The same procedure as for experiment 1 was used to calculate response-specific lateralization depending on visual feedback. Average waveform outcomes (C3–C4) for condition 2, 3, and 4 trials were subtracted from the average waveform outcomes (C3–C4) for the condition 1 trials, which yielded the 3 waveforms illustrated in Figure 4.

Right and left hand movements yielded a classic LRP (condition 1 vs. condition 2), whereas no LRP was observed when the electrophysiological activity under lateral or frontal mirror view conditions was subtracted from the activity under the direct view condition (condition 1 vs. condition 3 and condition 1 vs. condition 4). The amplitude of the LRP was determined as described in experiment 1. For the 2 waveforms that did not exhibit an LRP, the amplitude was calculated from 129 ms (mean onset latency for LRP) to 329 ms. Statistical analysis showed significant differences among amplitudes of the 3 waveforms ($F_{2,18} = 9.78, P = 0.001$). However, only the classic LRP differed significantly from the 2 waveforms for the lateral and frontal conditions ($P = 0.001$ and $P = 0.02$, respectively).

Although electrophysiological data cannot be compared between experiment 1 and 2 because of experimental differences, we observe a notable difference between the 2 experiments in the amplitude of classic LRPs (right and left hand conditions). In experiment 2, the magnitude of the LRP was only 40% of that observed in experiment 1. This difference reflects the different lighting conditions in the 2 experiments; in experiment 1, the task was performed in a lit room, whereas in experiment 2, the task was conducted in darkness. Electrophysiological measurements are highly sensitive to the physical properties of the stimulus, including the luminance, which may have affected the global amplitude of the EEG trace (see Luck 2005 for the ERP technique). Hence, luminance has a global effect on electrophysiological data. The fact that we recorded a classic LRP in both experiments whereas we
recorded a mirror induced LRP only in experiment 1 cannot be explained by a luminance effect.

Behavioral Results
Repeted-measures analysis of RTs showed no difference between conditions ($F_{2,18} = 0.26, P = 0.77$, see Tables 2).

Discussion
In experiment 2, performed in total darkness, we degraded the visual information of the hand in order to test whether motor cortex activation related to one limb relies more on body representation or visual information of the limb. Visual information about the hand position was provided by a set of LEDs fixed to a glove worn on the participant’s performing hand. In this condition, a classic LRP was observed for right and left hand movements. It should be noted that this LRP could be due solely to hand movements (i.e., not be related to any visual feedback) since it has been shown that vision of the hand is not necessary for generating this component (Coles 1989; Miller and Hackley 1992; Minelli et al. 2007) and, more importantly, since no LRP was observed in the lateral-view condition, in contrast to experiment 1. Hence, our results support our hypothesis since a representation of the hand, which was achieved by a structure-from-motion process, was not sufficient to yield cortical motor activity. These results are consistent with previous findings that have shown that the performance of a hand localization task differs with the amount of visual information provided about the position of the hand (Mon-Williams et al. 1997).

General Discussion
The aim of the present study was to determine if this motor cortical activation can be observed when the perception of limb movement is given by vision. Using an electrophysiological correlate of motor activation, partially generated in the MI (namely, the LRP), we found that viewing the position of one hand is sufficient to generate a cortical activity related to this hand, even if it is not the one that actually moves. Indeed, in experiment 1, we detected LRPs related to a hand seen in a sagittal mirror—indicating the presence of neural activity in the contralateral hemisphere related to this hand—while the other hand was active. Furthermore, we showed that this cortical activity does not depend on proprioceptive information since LRPs were recorded even when the apparent position of the hand in the mirror and the real position of the hidden hand were incongruent.

The present study also showed that this cortical motor activation only occurs when acute visual information about the hand is available. When the visual information of the hand in the mirror was reduced to small lights (experiment 2), yielding its representation by means of a structure-from-motion process, no motor activity was recorded in the cortical area of

Figure 4. (A–C) The 3 grand averaged waveforms and standard error of the mean ($N = 10$) from the 4 experimental conditions defined by the visual feedback on the performing hand in experiment 2 and their corresponding EMG (right and left hand) and EOG activity. Negative is plotted upward.
the inactive hand. These results indicate that cortical motor activity relies on the viewed image of the hand rather than on its actual position and that this cortical motor activity can be modulated by visual information.

The point along the perceptual processing pathway where cross-modal interactions take place is currently of great interest. Although some areas of convergence of multisensorial information have been localized in parietal areas, recent data from brain imaging studies suggest that cross-modal interactions occur at brain sites that were previously considered to be modality specific (Calvert et al. 1997, 1999). For example, an fMRI study has shown that tactile stimulation of a hand enhances activity in the visual cortex when the touched hand is on the same side as the visual stimulus (Macaluso et al. 2000). Based on the connectivity of brain areas, these authors argue that this enhancement is mediated via backprojections from multimodal cortical areas. In the present study, activity modulation in the motor cortex could have been generated through the visual system via parietal areas (dorsal visual stream) where visual and kinesthetic inputs converge. Interestingly, similar activity was recorded in the motor cortex when the viewed and actual positions were incongruent. In accordance with our hypothesis, the motor cortex activity appeared to rely strongly on visual information. These results are in agreement with those of electrophysiological studies in monkeys in that neurons with visual receptive fields centered on the animal’s arm can be activated by illusory visual information about hand position achieved with a fake arm (Graziano 1999). Data indicate that neurons in the premotor cortex are influenced by the position of the arm and that this influence is both visual and proprioceptive and that the 2 influences converge in single neurons. Our results are also in line with the action/observation matching process, well known as the neuron mirror system. First described in monkeys, area F5 (supposed to correspond to the Broca area in the frontal premotor cortex in humans) neurons have been shown to become active both when the animal performs a specific motor action and when it observes a similar act done by others (Rizzolatti et al. 1996).

Although, evidence indicate that the LRP reflect activity only in the MI, the presence of this component do not exclude an activation of premotor area in the condition of our experiment. Our results may also account for the presence of neuron within MI that are activated when observing one own’s movements. This would be in accordance with studies that have shown greater motor-evoked potentials recorded on hand muscles when MI is stimulated with transcranial magnetic stimulation while observing hands in a natural orientation to one’s own (Maeda et al. 2002).

It should be noted that none of the motor cortex activities related to a seen limb in the mirror conditions (presence of LRPs) depended on illusions of ownership of the hand seen in the mirror. Indeed, although participants did not have direct visual feedback on their real left hand (in the lateral mirror conditions), no ambiguity was possible, and all participants were aware of the presence of the mirror. A behavioral study has recently demonstrated that illusion of ownership is not a condition to bias proprioception (Holmes et al. 2006). Using a similar mirror paradigm to induce a conflict between vision and proprioception, these authors measured bias on reaching movements made with the hand hidden behind the mirror. They found that illusion of ownership of the seen hand was not strongly correlated with reaching performance. Thus, in the present study, the motor activity recorded in the contralateral brain area of the seen hand could reflect a relatively automatic process of adaptation to visual stimuli. In a other hand, our experimental setup with the lateral mirror may also induce some processes of motor imagery, that is, mental rehearsals of movements without actual execution. There is behavioral and neuropsychological evidence that motor sequence imagery and execution share common neural structures (Dominey et al. 1994; Decety 1996). Combined to these data, our results indicate that MI could be among these shared structures.

The absence of an LRP in the lateral mirror condition when the task was executed in experiment 2 is in agreement with previous behavioral studies that have found that subjects rely on what they feel rather than on what they see under dark conditions (Mon-Williams et al. 1997; Plooy et al. 1998). Degraded visual information about the hand might disrupt interaction between vision and proprioception, and thus, the image in the mirror would not be interpreted as a left hand by the central nervous system. The absence of an LRP in this particular condition supports our hypothesis, suggesting the importance of specific visual features (e.g., shape) and that visual capture is not possible when these specific features are not available.

The present study has revealed an electrophysiological correlate of visuo proprioceptive integration. To determine the position of the hand, one uses at least 2 types of cues: the felt position (proprioception) and the seen position (vision). When visual information concerning the apparent position of the hand is provided, the brain appears to automatically integrate that information even if it is not congruent with the proprioceptive information, suggesting that vision can bypass the peripheral information about limb position specified by muscle and joint receptors under certain circumstances. Unrestrained cortical motor activity due to visual information of hand position could be interpreted as an automatic process of recall that increases efficiency in particular visuomotor situations. This visual capture of proprioception has often been interpreted as the dominance of vision over proprioception. However, our results favor the presence of flexibility in the importance given to each modality (van Beers et al. 1999).


