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RESEARCH ARTICLE

Kinaesthetic mirror illusion and spatial congruence

Morgane Metral · Marie Chancel · Clémentine Brun · Marion Luyat · Anne Kavounoudias · Michel Guerraz

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Abstract Position sense and kinaesthesia are mainly derived from the integration of somaesthetic and visual afferents to form a single, coherent percept. However, visual information related to the body can play a dominant role in these perceptual processes in some circumstances, and notably in the mirror paradigm. The objective of the present study was to determine whether or not the kinaesthetic illusions experienced in the mirror paradigm obey one of the key rules of multisensory integration: spatial congruence. In the experiment, the participant's left arm (the image of which was reflected in a mirror) was either passively flexed/extended with a motorized manipulandum (to induce a kinaesthetic illusion in the right arm) or remained static. The right (unseen) arm remained static but was positioned parallel to the left arm's starting position or placed in extension (from 15° to 90°, in steps of 15°), relative to the left arm's flexed starting position. The results revealed that the frequency of the illusion decreased only slightly as the incongruence prior to movement onset between the reflected left arm and the hidden right arm grew and remained quite high even in the most incongruent settings. However, the greater the incongruence between the visually and somaesthetically specified positions of the right forearm (from 15° to 90°), the later the onset and the lower the perceived speed of the kinaesthetic illusion. Although vision dominates perception in a context of visuoproprioceptive conflict (as in the mirror paradigm), our results show that the relative weightings allocated to proprioceptive and visual signals vary according to the degree of spatial incongruence prior to movement onset.

Keywords Kinaesthesia · Spatial congruence · Mirror illusion · Multisensory integration

Introduction

Reflection of a moving hand in a mirror positioned in the sagittal plane (i.e. the plane that separates the left and right sides of the body) can give the illusion of symmetrical bimanual movements. Indeed, Guerraz et al. (2012) and Metral et al. (2013) observed that mirror reflection of an arm moved passively by a motorized manipulandum induces consistent, vivid kinaesthetic illusions of movement of the hidden, static arm in the direction of mirror displacement. The occurrence of this visually induced kinaesthetic illusion confirms that visual afferents are of prime importance in sensing both limb position and limb movement.

However, position sense and kinaesthesia are not exclusively derived from visual afferents; somaesthetic afferents (notably type Ia and II sensory endings; Goodwin et al. 1972; Teasdale et al. 1993; for a review, see Proske and Gandevia 2012) and cutaneous afferents (Collins and

M. Metral · M. Chancel · C. Brun · M. Guerraz
LPNC, CNRS, Univ. Savoie Mont Blanc, 7300 Chambéry, France

M. Metral · M. Luyat
PSITEC, Univ. Lille, 59653 Villeneuve d'Ascq, France

M. Chancel · A. Kavounoudias
LNIA UMR 7260, Aix-Marseille Univ. CNRS, Marseille, France

M. Guerraz (✉)
Laboratory of Psychology and NeuroCognition,
UMR 5105, CNRS – University Savoie Mont Blanc,
BP 1104, 73011 Chambery Cedex, France
e-mail: Michel.guerraz@univ-savoie.fr

Prochazka 1996; Blanchard et al. 2011, 2013) also make significant contributions. Unsurprisingly, mirror manipulation has an even greater impact when proprioceptive afferents are weakened or perturbed. For example, Guerraz et al. (2012) showed that degradation of proprioceptive afferents by the application of diffuse vibration to the hidden arm (which is known to degrade position perception and movement control; Roll et al. 1989; Cordo et al. 1995; Bock et al. 2007) both reduced the latency of the visually induced kinaesthetic mirror illusion and increased its strength. In contrast, when the proprioceptive signal conflicts with the visual signal (for instance when the reflected arm is moving in a direction opposite to the simulated stretch induced by muscle vibration), the percept is often situated midway between each channel considered separately. Indeed, Tsuge et al. (2012) and Guerraz et al. (2012) showed that opposing mirror and vibration illusions tended to cancel each other out, whereas congruent mirror and vibration illusions reinforced each other. These results confirm that spatial congruence (as temporal coincidence) is a key factor for merging multisensory signals (Pavani et al. 2000; Maravita et al. 2003; Austen et al. 2004).

The objective of the present experiment was to further investigate visual and proprioceptive integration in the context of kinaesthesia. In particular, we sought to determine whether (and how) proprioceptive and visual afferents in the mirror paradigm are co-processed and integrated when the degree of incongruence between the "visual" and "proprioceptive" arms prior to onset movement increases. In contrast to the above-mentioned literature experiments, the proprioceptive signals from the hidden hand were neither degraded nor stimulated by the use of vibrators: "real" signals came from a hidden arm that was static and held either in a flexed position (i.e. the same as the initial position of the passively moved mirror hand) or extended by up to 90°. We then measured the kinaesthetic illusion's occurrence, onset and speed as a function of the degree of congruence between the initial positions of the "visual" and "proprioceptive" arms.

Method

Participants

Seventeen healthy adult participants (12 females and 5 males; 2 left-handed and 15 right-handed) took part in the experiment. The mean ± SD age was 23.7 ± 3.7 (20–32) years. None of the participants had a history of visual, proprioceptive or neuromuscular disease. All the participants provided written, informed consent prior to initiation of the experiment. Three of the 17 participants failed to experience a mirror illusion in the familiarization phase of the experiment in which the mirror reflection of the left forearm coincided with the true position of the right arm prior to movement onset. Those three participants were therefore excluded from the study. The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and was approved by the local independent ethics committee (University of Savoie, Chambery, France; reference: UDS 2013025), and informed consent was obtained from all individual participants included in the study.

Material

Participants sat in front of a large, custom-built box (Fig. 1). A mirror measuring 65 × 65 cm was positioned vertically in the middle of the box, with the reflective surface facing the participant's left arm and oriented parallel to his/her midsagittal axis (Fig. 1). The participant's forearms were positioned on each side of the mirror and were supported by two manipulandum devices. The distances between the manipulanda and the mirror were adjusted so that the mirror image of the left arm coincided with the position of the right arm. Each manipulandum consisted of a wooden arm (on which the participant positioned his/her forearm) and a hand grip at the end of the wooden arm. The left manipulandum was fitted with a low-noise DC electric motor and could flex (via a remote control) the participant's left forearm from an initial starting position of 30° to the horizontal (Fig. 1). The manipulandum's angular speed was fixed at 3.8°/s. The participant's forearm was adjusted on the manipulandum so that the motorized device's axis of rotation coincided exactly with the participant's elbow joint. The right manipulandum did not move during the trial itself. However, prior to each trial, the right manipulandum could be either positioned parallel to the left manipulandum's starting position or placed in extension (from 15° to 90°, with steps of 15°) relative to the left manipulandum's starting position. Hence, when the left and right forearms were parallel (i.e. with a difference of 0°), the mirror reflection of the left forearm (specified by visual afferents) coincided with the true position (specified by somaesthetic afferents) of the right forearm prior to movement onset. In all the other right forearm positions (15°, 30°, 45°, 60°, 75° and 90°), the visually and somaesthetically specified positions of the right forearm conflicted.

Participants were told to use their right foot to indicate the time course and speed of illusory movement felt in their right arm. To this end, the participant's right foot was taped to a foot pedal, the rotational axis of which was close to the heel. To increase the range of foot motion (which was rather limited in some participants), the

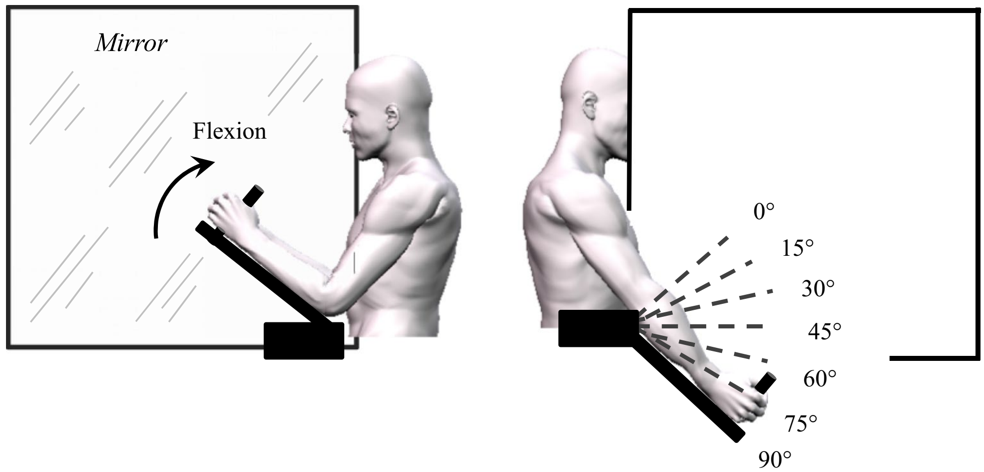


Fig. 1 The mirror box set-up. The participant sat at a table and faced a box that was compartmentalized by a mirror reflecting the image of his/her left arm. The manipulandum supporting the left arm was motorized and could flex the left arm at an angular speed of 3.8°/s. The right arm was out of sight, static and could be positioned either in the same initial position as the left arm (i.e. the congruent position: 0°) or extended by up to 90° (i.e. the incongruent positions)

participant's right leg was in slight extension. The displacements of the left manipulandum and the foot pedal were recorded with an electromagnetic motion capture system (Polhemus Fastrak™, Colchester, VT, USA). A sensor was positioned on each device so as to continuously record the manipulandum and foot angles (sampling frequency: 60 Hz).

Procedure

Throughout the experiment, the participants were required to look at the reflection of their left arm in the mirror. The left arm remained visible in peripheral vision and the right arm was always hidden. Following a baseline, movement-free epoch of ~5 s, the left forearm was passively flexed for duration of ~10 s and at a constant angular speed of 3.8°/s, from its starting position (30° from horizontal) to a final position of ~70°. Each trial consisted of one discrete arm movement in flexion. Participants were told not to resist this passive displacement. Prior to each trial, participants performed active, synchronous, flexion–extension movements of both arms. This gave the two arms similar immediate histories of contraction and length changes before the trials.

Each of the seven conditions (i.e. with an angle mismatch of 0°, 15°, 30°, 45°, 60°, 75° and 90°, respectively, in the starting position) was repeated four times in pseudorandom order, giving a total of 28 trials per participant. Furthermore, control trials (in which the left hand was static) were performed in all starting positions. No illusions were reported for the control trials, and so the latter were not included in the statistical analysis.

Quantification of the kinaesthetic illusion

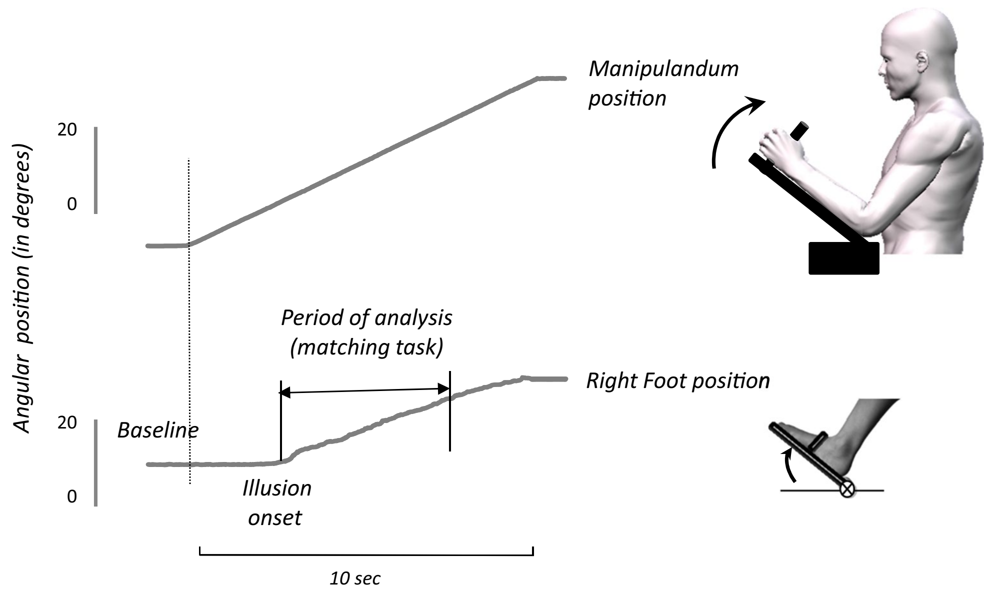
Subjective reporting

At the end of each trial, participants were required to verbally rank the speed of the illusory displacement of the right arm on an integer scale from 0 to 20. Zero corresponded to the absence of illusory displacement, 10 corresponded to the same speed of displacement as for the passively moved left forearm, and 20 corresponded to twice the speed of the passively moved left forearm. In order to familiarize themselves with this subjective rating of displacement speed, the subjects rated trials with passive displacement of the left forearm prior to the experimental session itself. To ensure that participants report precisely their kinaesthetic sensations and do not respond as to whether the arm moved physically or not, they were informed that the right arm did not physically move in experimental trials.

"Foot-matching"

During each trial, the participant was told to use his/her right foot to indicate what he/she felt in his/her right arm (see Guerraz et al. 2012). The foot-matching task was used to measure the illusory movement's onset and speed (in °/s). The onset was defined as the time point at which the angular position of the foot was more than two standard deviations from the mean baseline position (calculated over a 1-s epoch prior to movement of the manipulandum). The speed of illusory movement was calculated as the average speed of angular foot displacement during the 5-s time period following onset of the illusion (see Fig. 2). This

Fig. 2 The *upper graph* shows passive rotation of the left arm (flexion) by the manipulandum. The *lower graph* represents a typical right foot-matching adjustment, from which the onset and speed of illusory movement were calculated



short time period was chosen because some participants reached their maximum (limited) angular movement capacity rather quickly. When no illusion occurred, the speed of the illusory movement was zero (0°/s). Given the unusual nature of the foot-matching task, participants performed familiarization trials prior to the experimental session.

Statistics

A Chi-squared test was used to compare the frequency of illusion occurrence under the various experimental conditions. Data from the matching task (onset and speed) and subjective reporting were analysed in a one-way, repeated-measures analysis of variance (ANOVA) with seven modalities of the "congruence factor" (0°, 15°, 30°, 45°, 60°, 75° and 90°). The reported values were Huynh–Feldt corrected. A Holm post hoc correction was applied for multiple comparisons. The threshold for statistical significance was set to $P < 0.05$.

Results

Illusion occurrence

Reflection of the passively moving left arm in the mirror evoked a kinaesthetic illusion of right arm displacement in the same direction, i.e. a mirror illusion. When the initial positions of the reflected left arm (the mirror arm) and the right arm were congruent [i.e. no angular difference (0°) in the reference condition], the illusion occurred in 96.67 per cent of the trials. The frequency of the illusion decreased as the incongruence between the reflected left arm and the hidden right arm grew but remained quite high, even in the most incongruent setting (the 90° difference, with a frequency of 64 %). Statistical analysis (with a Chi-squared test) indicated that the frequency of occurrence in the 90° condition differed significantly from the frequencies in all conditions ($P < 0.05$) other than the 75° condition. In turn, the 75° condition differed significantly from the other experimental conditions. There were no significant differences between the other five experimental conditions (0°, 15°, 30°, 45° and 60°).

The speed of illusory movement (subjective rating)

When the two arms were in the same position (i.e. a difference of 0°) prior to passive displacement of the left arm, the mean ± SD subjective rating of illusory movement was 8.11 ± 2.2. Hence, the hidden right arm was perceived as moving about 20 % more slowly than the left arm (and its mirror reflection). As can be seen in Table 1, the mean rating fell linearly ($y = -0.84 + 9.3$ $r^2 = 0.96$) with increasing incongruence. The mean rating was 2.9 ± 3.1 when the initial position of the two arms differed by 90° (i.e. maximum incongruence). The ANOVA confirmed the significant effect of congruence on the subjective speed rating [$F(6, 78) = 24.02$, $P < 0.001$, $\eta_p^2 = 0.64$]. A post hoc pairwise analysis (Table 1) indicated that the larger the degree of incongruence, the greater the likelihood of a significant difference. Although the 0°, 15° and 30° conditions did not differ from each other, they all differed significantly from the 60°, 75° and 90° conditions.

To ensure that the reduction in the speed of the mirror illusion was not solely due to mixing trials in which illusion occurred and trials in which illusion did not occur (with a subjective rating of 0 in the latter cases, the number

Table 1 Characteristics of the kinaesthetic illusions (occurrence, subjective reporting, foot-matching and onset) for each "congruence factor" (0°, 15°, 30°, 45°, 60°, 75° and 90°)

	0°	15°	30°	45°	60°	75°	90°
Frequency of occurrence (%)	96	98	93	96	89	80	64
Mean subjective speed (SD)	8.11 (2.22)	7.71 (2.30)	7.04 (2.55)	6.34 (1.90)	5.30 (2.59)	4.59 (3.15)	2.91 (3.13)
Mean foot speed (°/s) (SD)	2.76 (1.60)	2.83 (1.63)	2.28 (1.46)	2.41 (1.23)	2.22 (1.57)	1.49 (1.34)	0.98 (1.20)
Gain	0.73	0.75	0.6	0.63	0.58	0.39	0.26
Mean latency of onset in seconds (SD)	1.65 (0.86)	1.87 (1.05)	1.89 (1.17)	2.21 (143)	2.47 (1.60)	2.51 (1.69)	3.01 (1.73)
Subjective reports comparisons							
0°	/	ns	ns	*	***	***	***
15°	ns	/	ns	.	***	***	***
30°	ns	ns	/	ns	*	***	***
45°	ns	ns	ns	/	ns	*	***
60°	ns	ns	ns	ns	/	ns	***
75°	**	***	ns	.	ns	/	*
90°	***	***	**	***	**	ns	/

The gain of the foot speed response is also reported (i.e. the ratio between the foot speed and the left arm speed, the image of which was reflected in the mirror). A gain of 1 would indicate that the measured foot speed and of passive displacement of the left arm's speed were equal. A positive gain indicates that the response was oriented in keeping with the mirror stimulation. We performed post hoc multiple comparisons with Holm correction of subjective reports and foot-matching. The threshold for statistical significance was set to $P < 0.05$

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; · $P < 0.1$; *ns* non-significant

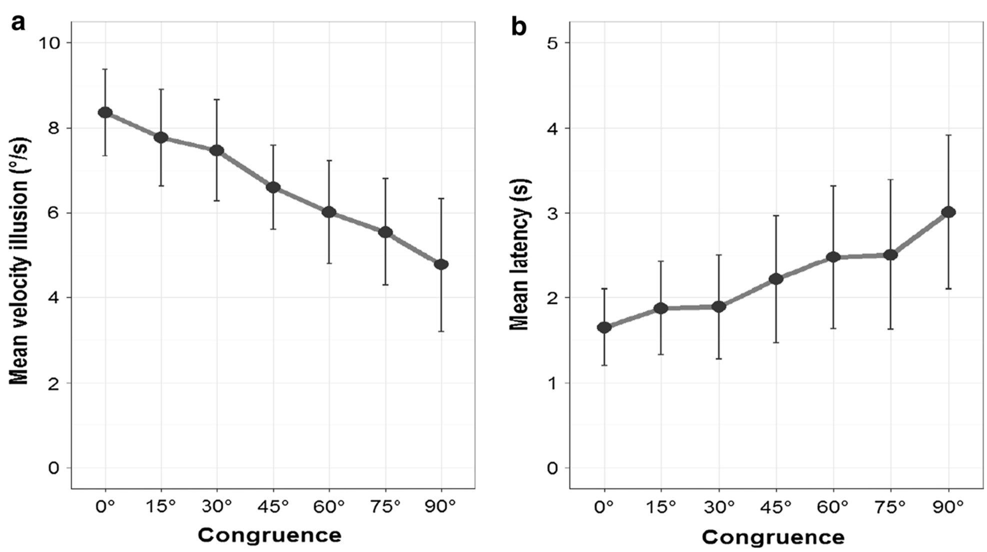


Fig. 3 Mean subjective speed (*left panel*) and mean latency (*right panel*) of the kinaesthetic illusion, as a function of the degree of incongruence between the initial positions of the left and right arms. These data only concerned trials in which an illusion occurred. The *error bars* correspond to 95 % confidence intervals

of which increased with the degree of incongruence), we then limited our analysis to trials in which a mirror illusion had occurred. Given our within-subjects design, participants who did not experience any illusory displacement in one of the seven congruence modalities could not be included in the analysis. This additional ANOVA (involving 10 participants among the 14 involved in the experiment) confirmed that the greater the degree of incongruence between the two arms, the slower the perceived displacement [$F(6, 54) = 13.3$, $P < 0.001$ $\eta_p^2 = 0.59$]. Those results are reported in Fig. 3a.

The speed of illusory movement (foot-matching)

An analysis of the foot-matching data yielded much the same results as the analysis of subjective rating: the mean speed of angular foot displacement decreased as the incongruence increased [$F(6,78) = 9.46$, $P < 0.001$, $\eta_p^2 = 0.42$]. A post hoc analysis revealed that the mean speed of angular foot displacement was lower in the 75° and 90° conditions than in the more congruent 0° to 60° conditions ($P < 0.05$). There were no significant differences between the 0°, 15°, 30°, 45° and 60° conditions; this may have been due to the difficulty of using the foot to precisely report on perception in the arm. However, the gain of the foot speed response (calculated in terms of the ratio between the foot speed and the subjective rating of arm displacement through the mirror) decreased markedly from the 0° condition (gain: 0.73) to the 90° condition (gain: 0.26). A supplementary analysis of foot-matching speed (based on the 10 participants who experienced illusory displacements whatever the experimental condition) yielded similar results [$F(6, 54) = 5.1$, $P < 0.01$, $\eta_p^2 = 0.35$].

The latency of illusory movement onset

Only trials in which an illusion occurred could be considered in the latency analysis, and so only participants who did experience illusory displacement in the seven congruence modalities were included in the statistical analysis. The mean latency of the illusory movement increased as the degree of incongruence between the two arms increased [$F(6, 54) = 10.1$, $P < 0.001$, $\eta_p^2 = 0.52$], with mean latencies of 1.65 s in the 0° condition and 3.01 s in the 90° condition Fig. 3b.

Discussion

In the present experiment, participants frequently reported illusory displacements of their static, right, unseen forearm when looking at the mirror reflection of their passively moved left forearm (i.e. a mirror kinaesthetic illusion). This attests to the significant involvement of visual afferents in kinaesthesia (Maravita et al. 2003; Mercier and Sirigu 2009; Holmes et al. 2004). Although vision largely dominated the percept, the present results showed that the occurrence, latency and speed of illusory movement were modulated by the congruence conditions. Greater spatial/directional incongruence between the initial position of the mirror hand and that of the unseen proprioceptive hand was associated with a lower frequency of illusory movement, a greater latency and a lower speed of illusory movement.

The impact of spatial congruence has been thoroughly investigated in the context of the "rubber hand" body ownership illusion; when a dummy hand is stroked with a brush, the participant feels brushstrokes on their own (hidden) hand. During synchronous visual and tactile stimulation, participants may come to feel that the rubber hand is part of their own body (Tastevin 1937; Botvinick and Cohen 1998). Several researchers have reported that the illusion survives small mismatches between the position of the fake (viewed) hand and the subject's proprioceptive hand but is abolished when the fake hand is in an anatomically implausible posture (Pavani et al. 2000; Maravita et al. 2003; Austen et al. 2004; Costantini and Haggard 2007). Similarly, psychophysical studies using wedge prisms (Hay and Pick 1966; Warren 1980) have revealed that as long as the conflict between visual and proprioceptive cues was not too great, subjects usually perceived their hand to be closer to the visually specified position than the proprioceptively specified position. Our present results show that what holds true for body ownership and limb position sense also applies to kinaesthesia. We found that vision dominated the kinaesthetic percept (although not completely; see Guerraz et al. 2012) in conditions with no incongruence (0°) or just a slight (15°) incongruence between the initial visual and proprioceptive signals. However, the kinaesthetic illusion gradually faded as the mismatch (incongruence) between visual and muscle-proprioceptive signals increased; the greater the incongruence between the initial position of the visual and proprioceptive arms, the weaker the illusion. In other words, passive displacement of the mirror arm is more likely to evoke a fast kinaesthetic illusion when the visual and proprioceptive signals derive from the same arm prior to movement (i.e. when the reflected left hand appears to occupy the space of the right hand). Of particular interest, the frequency of the illusion remained quite high even in the most incongruent setting (the 90° difference, with a frequency of 64 %). These results indicate that as long as visual and proprioceptive afferents remains anatomically plausible (as was the case in our experiment), visual and proprioceptive signals are continuously integrated for speed estimates of arm movement. However, as the incongruence grows, the weighting allocated to proprioceptive afferents (attesting to a static arm) increases and the weighting allocated to visual afferents (attesting to a moving arm) decreases.

There are several possible explanations for the high frequency of illusions in conditions with marked mismatch between the visual and proprioceptive arms. Firstly, several researchers have reported that the central nervous system is not highly conscious of proprioceptive afferent signals (Mon-Williams et al. 1997; Fourneret and Jeannerod 1998) and therefore slow arm displacements (Hall and McCloskey 1983) or proprioceptive drift (the proprioceptive sense that the hidden hand is moving towards the viewed hand) occurring over timescales as short as a few seconds (Wann and Ibrahim 1992; Holmes and Spence 2005). In contrast to the above-mentioned rubber hand experiments (Austen et al. 2004; Pavani et al. 2000), the visual hand in our mirror paradigm was never in an implausible posture what allows multisensory integration to occur. Furthermore, Formaggio et al. (2013) recently reported that passive displacement of the arm per se can induce bilateral activation of the motor loci (i.e. event-related desynchronization). More generally, it has been found that unimanual active motor tasks involve not only the contralateral primary motor cortex but also the ipsilateral primary motor cortex in asymmetrical way; in right-handed subjects, activation of the left hemisphere during left hand movements is greater than activation of the right hemisphere during right hand movements (Ziemann and Hallett 2001; Van den Berg et al. 2011; Beaulé et al. 2012). Given that, (1) most of the participants in the present study were right-handed participants and (2) only the non-dominant left arm was moved passively, our experiment conditions may have facilitated the sensation of illusory movement of the contralateral (right) arm.

Taken as a whole, the present results showed that visual and proprioceptive signals can be combined to offer a coherent, unified percept. Although purely visual information can dominate slightly discrepant proprioception (as reported previously for the rubber hand illusion), proprioception may reduce the impact of visual information about hand position when the latter is strongly incongruent (Maravita et al. 2003). It is noteworthy to mention that in the present experiment, the arm was passively moved by a motorized manipulandum avoiding central motor commands. However, central (efferent) signals as well as afferent signals contribute to kinaesthesia and position sense (Gandevia et al. 2006; Metral et al. 2013; Romano et al. 2013). For instance, Romano et al. (2013) showed, using the mirror paradigm, that active displacements of a finger induce larger mirror effects than passive displacements. In that respect one might expect that active movements (and efferent signals) combined with visual signals (mirror reflection of the moving hand) might dominate to a larger extent discrepant proprioception in our experimental paradigm.

Our present results confirm that the spatial congruence of afferent signals (at least in the absence of efferent signals) is an important aspect of multisensory integration and for the adjustment of the relative weightings of multiple kinaesthetic cues. From a clinical point of view, the fact that a kinaesthetic mirror illusion may be generated even with a postural mismatch between the mirror arm and the hidden arm, might account for pain relief reported in patients who experience a phantom holding painful posture that could not possibly be matched by the intact limb.

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Conflict of interest None of the authors have any conflicts of interests.

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