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RESEARCH ARTICLE

The kinaesthetic mirror illusion: How much does the mirror matter?

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Abstract The reflection of a moving hand in a mirror positioned in the sagittal plane can create an illusion of symmetrical, bimanual movement. This illusion is implicitly presumed to be of visual origin. However, muscle proprioceptive afferents of the arm reflected in the mirror might also affect the perceived position and movement of the other arm. We characterized the relative contributions of visual and proprioceptive cues by performing two experiments. In Experiment 1, we sought to establish whether kinaesthetic illusions induced using the mirror paradigm would survive marked visual impoverishment (obtained by covering between 0 and 100 % of the mirror in 16 % steps). We found that the mirror illusion was only significantly influenced when the visual degradation was 84 % or more. In Experiment 2, we masked the muscle proprioceptive afferents of the arm reflected in the mirror by co-vibrating antagonistic muscles. We found that masking the proprioceptive afferents reduced the velocity of the illusory displacement of the other arm. These results confirm that the mirror illusion is not a purely visual illusion but emerges from a combination of congruent signals from the two arms, i.e. visual afferents from the virtually moving arm and proprioceptive afferents from the contralateral, moving arm.

Keywords Kinaesthesia · Mirror illusion · Muscle proprioception · Visual impoverishment

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. The mirror paradigm was initially developed to treat phantom limb pain in unilateral amputees (Ramachandran et al. 1995) but has also been used over the last two decades as a rehabilitation tool for promoting recovery from hemiparesis (Ramachandran and Altschuler 2009; Rosen and Lundborg 2005; Dohle et al. 2009; Guerraz 2015). More recently, experiments conducted in healthy participants showed 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 the mirror displacement (Guerraz et al. 2012; Tsuge et al. 2012; Metral et al. 2015). The occurrence of this visually induced kinaesthetic illusion indicates that visual afferents might be of prime importance in sensing limb movement (i.e. kinaesthesia).

However, kinaesthesia is not exclusively derived from visual afferents; muscle spindle 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 Prochazka 1996; Blanchard et al. 2011, 2013) also make significant contributions. For instance, it has been shown that the mirror illusion is less intense when the unseen arm is not in the same position as the reflected arm (Metral et al. 2015). Likewise, masking the proprioceptive afferents of the unseen arm

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increases the illusory velocity of displacement (Guerraz et al. 2012).

Although the muscle proprioceptive afferents of the arm subjected to the kinaesthetic illusion have received much attention, this is not the case for the proprioceptive afferents originating from the other (moved) arm. However, it has recently been reported that manipulating the muscle proprioceptive afferents of one arm affects not only the motor behaviour of the other arm (Ridderikhoff et al. 2006; Brun et al. 2015; Brun and Guerraz 2015) but also the latter's perceived position and perceived movement (Izumizaki et al. 2010; Hakuta et al. 2014; Kuehn et al. 2015). For instance, Izumaki et al. (2010) showed that stimulating the muscle proprioceptive afferents of one arm (by the application of tendon vibration to either the flexor or extensor muscles) modified the perceived position of the other arm. The "bimanual integration of proprioceptive afferents" (Kuehn et al. 2015) might well contribute to the occurrence and intensity of the kinaesthetic illusions reported in the mirror paradigm. Hence, the kinaesthetic illusions evoked in the mirror paradigm might well be of both visual and proprioceptive origin.

To determine the relative contributions of visual and muscle cues, we performed two experiments. Experiment 1 consisted in testing whether the kinaesthetic illusions induced by the mirror paradigm would survive marked visual impoverishment obtained by covering between 0 and 100 % of the mirror in 16 % steps. Conversely, Experiment 2 was designed to estimate the relative contribution of visual cues by masking muscle proprioceptive afferents (through co-vibration of antagonistic muscles) of the arm reflected in the mirror. Indeed, we know that when vibration is applied concurrently on a muscle that is passively lengthened or shortened, it degrades afferent proprioceptive responsiveness since the primary ending activity is then predominantly driven at the vibration frequency and any frequency modulation related to the imposed movement disappears (Roll et al. 1989). The masking effect of the vibration seems also responsible for the impairment in position and force perception observed during a full whole-body exposition to vibration (Ribot et al. 1986). Finally, co-vibrating two antagonist muscles at the same frequency does not elicit any movement perception (Gilhodes et al. 1986) and alters sensorimotor tasks such as matching position task or haptic shape perception task (Bock et al. 2007). We therefore hypothesized that if muscle proprioceptive inputs from the moving arm influence the contralateral kinaesthetic illusion evoked in the mirror paradigm, the latter illusion would be less intense when the proprioceptive afferents of the reflected arm are mostly masked by co-vibration.

Methods

Participants

Nineteen healthy adult participants (14 females and 5 males; 16 right-handed; mean ± SD age 21.7 ± 1.6 years) took part in Experiment 1 and eighteen healthy adult participants (16 females and 2 males; 15 right-handed; mean ± SD age 20.9 ± 5.9 years) took part in Experiment 2. Three of the 19 participants in Experiment 1 and 3 of the 18 participants in Experiment 2 failed to experience a mirror illusion during the experiment's familiarization phase and were therefore excluded from the studies. None of the participants had a history of visual, proprioceptive or neuromuscular disease. All the participants provided their written informed consent prior to initiation of the experiment. 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 Savoie Mont Blanc, Chambery, France; reference: UDS 2013025).

Materials

Participants sat in front of a large, custom-built box. 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. The participant's forearms were positioned on each side of the mirror and were supported by two manipulanda. 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 right manipulandum did not move, while the left manipulandum was fitted with a low-noise DC synchronous motor (220 v, Crouzet™ France) and could flex or extend (via a remote control) the participant's left forearm from the initial starting position (Fig. 1). The manipulandum's angular speed was always 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 elbow joint.

Participants were told to lift their right foot to indicate the onset of illusory movement. To this end, the participant's right foot was taped to a foot pedal, the rotational axis of which was close to the heel. The displacements of the left manipulandum and the foot pedal were recorded with an electromagnetic motion capture system (Fastrak™, Polhemus, Colchester, VT, USA). A sensor was positioned

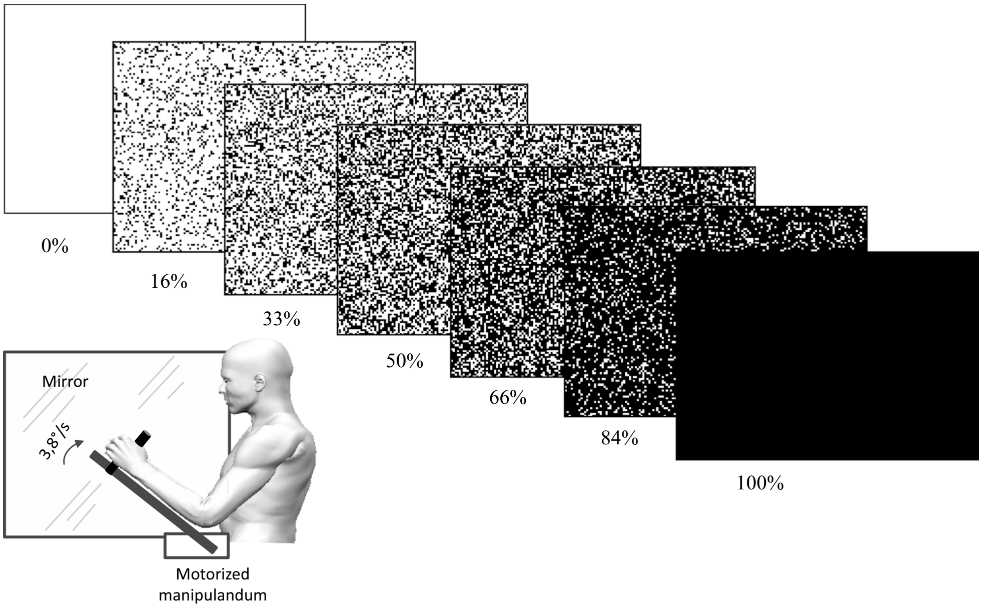

Fig. 1 Mirror box set-up (*lower panel*) and the different pixel densities used to create the visual impoverishment conditions in Experiment 1 (from 0 to 100 %)

on each device so as to continuously record the manipulandum and foot angles (sampling frequency: 60 Hz).

Procedure

Experiment 1

Throughout the experiment, the participants were required to look at a fixation cross in the centre of the mirror. The right arm was always hidden. Before each trial, the two arms were positioned at an angle of 30° to the horizontal. Following a baseline, movement-free epoch of ~5 s, the left forearm was passively flexed at a constant angular speed of 3.8°/s (total duration of movement: ~8 s). Participants were told not to resist this passive displacement.

Visual impoverishment was performed by affixing different plastic sheets to the mirror (Fig. 1). The sheets contained variable densities of randomly positioned black pixels (1.85 × 1.85 mm). Sheets were generated with a VBA script in PowerPoint software (Microsoft Visual Basic 7.1®). Overall, the black pixels covered 0, 16, 33, 50, 66, 84 or 100 % of the mirror's surface area. Each of these seven visual conditions was repeated four times in pseudorandom order, giving a total of 28 trials per participant. Four sham trials were performed with the eyes closed. Participants performed active, synchronous, flexion–extension movements of both arms before each trial. This allowed the two arms to have similar immediate history of contraction and length changes before trials (Gregory et al. 1988; Proske et al. 1993). Following these movements, the two arms were re-positioned at an angle of 30 ° to the horizontal before the next trial.

Experiment 2

In Experiment 2, participants were required to look at a fixation cross in the centre of the mirror. In contrast to Experiment 1, the mirror was not obscured by black pixels (i.e. it corresponded to the 0 % impoverishment condition from Experiment 1). The right arm was always hidden behind the mirror. Before each trial, the two arms were positioned at an angle of 45° to the horizontal. Following a baseline, movement-free epoch of ~5 s, the left forearm was passively flexed or extended at a constant angular speed of 3.8°/s (total duration of movement: ~8 s). An electromechanical vibratory apparatus (Innovative Technology, France) was attached to the left biceps and triceps with elastic bands. Microneurographic studies (the recording of afferent units via a microelectrode inserted in a human superficial nerve) have shown that low-amplitude vibration preferentially activates muscle spindle endings; this masks the spontaneous discharges recorded in the absence of vibratory stimulation (Roll et al. 1989). In half of the trials, the muscle afferents of the left arm were masked by switching on the vibrators (frequency: 40 Hz) immediately before the arm was passively moved. When the trial had finished, the vibrators were switched off. A frequency of 40 Hz was chosen because it is an optimal stimulation to completely mask natural discharges of muscle spindle endings that would otherwise be observed in response to the passively imposed movement of the arm, as evidenced by microneurographic and psychophysical studies (Roll et al. 1989; Cordo et al. 1995). This level of vibration frequency was also low enough to be bearable for the duration of the experiment. Some sham trials ($n = 8$) without a mirror were included; only the left arm was visible and the mirror was covered by an opaque board (with a fixation cross at its centre). The two movement conditions (flexion vs. extension) were paired with two masking conditions (masking vs. no masking), giving a total of four experimental conditions in a within-subjects design. Each condition was repeated four times in pseudorandom order, giving a total of 16 true trials (and 8 sham trials) per participant. No vibration was applied during sham trials. Participants were asked to move both arms freely and synchronously for a few seconds at the end of each trial.

Quantification of the kinaesthetic illusion

Subjective reporting

At the end of each trial, participants were required to verbally rate the speed of the illusory displacement of the right arm on an integer scale from 0 to 20: a rating of 0 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 several trials with passive displacement of the left forearm prior to the experimental session itself. Velocity of passive displacement was always set at 3.8°/s.

“Illusion onset”

During each trial, the participant was told to use his/her right foot to indicate when he/she felt the sensation of right arm movement. To do so, the participant was required to lift his/her right foot (Fig. 2). 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 onset includes both the delay for the illusion to occur and the time for initiating foot movement (motor response time). Given the unusual nature of the foot-matching task, participants performed familiarization trials prior to the experimental session. Despite this familiarization phase, a few participants almost always forgot to report the illusion onset. Hence, only subjective ratings could be analysed for these participants.

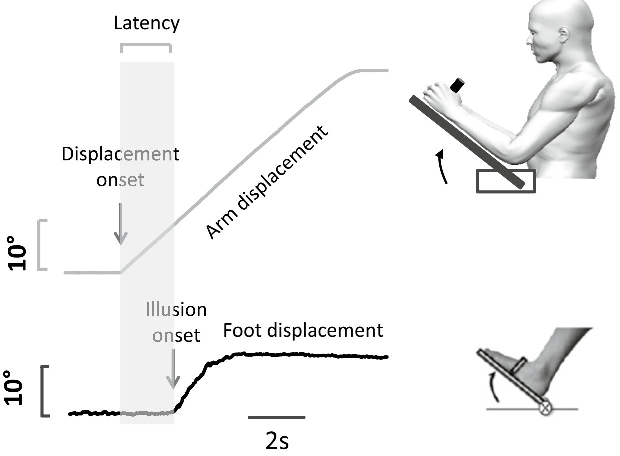

Fig. 2 Illusion onset quantification. The *upper* trace depicts the passive (motorized) displacement of the *left arm* intro flexion. The *lower* trace shows a typical foot response in response to illusion appearance. The width of the *grey bar* represents illusion latency

Statistics

In Experiment 1, a Chi-squared test was used to compare the various experimental conditions in terms of the frequency of illusion occurrence. The onset latency and subjective rating were analysed in a one-way, repeated-measures analysis of variance (ANOVA) with seven modalities (0, 16, 33, 50, 66, 84 and 100 %) in Experiment 1 and a two-way, repeated-measures ANOVA with movement (flexion vs. extension) and proprioceptive masking (masking vs. no masking) as independent variables in Experiment 2. For these ANOVA, we considered the mean latency and mean rating from the trials in each experimental condition and for each participant. 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 $p < .05$.

Results

Experiment 1

Occurrence of the mirror illusion

Reflection of the passively moving left arm in the mirror evoked in most individuals a kinaesthetic illusion of right arm displacement in the same direction, i.e. a mirror illusion. Among 19 individuals who consented to participate, 16 experienced such an illusion in our pretest phase. Since the purpose of the Experiment was to study this illusion phenomenon, only those latter 16 individuals could take

Table 1 Occurrence and subjective rating for each "visual impoverishment condition" (0, 16, 33, 50, 66, 84 and 100 % eyes closed—sham)

	0 %	16 %	33 %	50 %	66 %	84 %	100 %	Eyes closed
Frequency of occurrence (%)	90.6	95.3	95.3	95.3	85.9	87.5	40.6	35.9
Mean subjective speed (SD)	7.22 (2.78)	7.67 (1.63)	6.66 (2.12)	6.78 (2.43)	5.30 (2.83)	4.42 (2.27)	0.81 (1.05)	0.88 (1.15)

Comparisons of subjective ratings

	0 %	16 %	33 %	50 %	66 %	84 %	100 %
0 %	/	ns	ns	ns	**	**	**
16 %	1.000	/	ns	ns	**	**	**
33 %	0.943	0.236	/	ns	ns	**	**
50 %	1.000	0.371	1.000	/	*	**	**
66 %	0.001	0.000	0.039	0.019	/	ns	**
84 %	0.000	0.000	0.000	0.000	0.371	/	**
100 %	0.000	0.000	0.000	0.000	0.000	0.000	/

Mean subjective ratings represent the mean values of the 16 participants involved in Experiment 1. We performed post hoc multiple comparisons (with Holm correction) of subjective ratings. The threshold for statistical significance was set to $p < .05$

** $p < .01$; * $p < .05$, *ns* not significant

part to Experiment 1. Results showed that even in those 16 participants, illusion did not occur in all trials when the mirror was not obscured at all (visual impoverishment: 0 %) but did still occur in 90.6 % of them (Table 1). Interestingly, the illusion occurrence rate remained high (>85 %) in those participants in the other visual impoverishment conditions—even in the 84 % condition. The illusion occurrence rate only dropped when the mirror was completely obscured by black pixels. Even then (i.e. when no mirror feedback was available), an illusion was reported in 40.6 % of the trials. This value is similar to the rate of 36 % observed in the sham "eyes closed" trials. A statistical analysis indicated that only the illusion occurrence rate in the 100 % condition and "eyes closed" conditions differed significantly from that observed in the 0 % condition ($p < .05$).

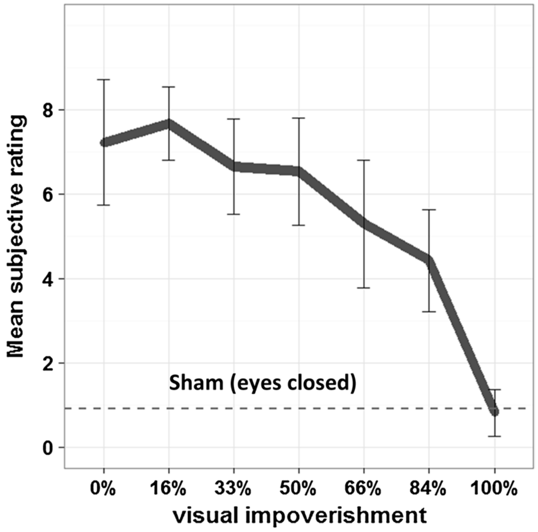

Fig. 3 Mean subjective speed ($n = 16$) of the kinaesthetic illusion, as a function of the degree of visual impoverishment. The *dashed line* represents the mean subjective rating observed in the sham trials, that is, when participants closed their eyes. The *error bars* correspond to 95 % CIs

The speed of illusory movement (subjective rating)

In the 0 % visual impoverishment condition, the mean ± SD subjective rating of illusory movement was 7.2 ± 2.8. Hence, the hidden right arm was perceived to be moving about 30 % slower than the left arm (and its mirror reflection). As can be seen in Table 1 and Fig. 3a, the mean rating remained fairly constant up to a visual impoverishment condition of 50 %, decreased slightly in the 66 and 84 % conditions and dropped to a value of 0.8 ± 1.05 for the 100 % condition. An ANOVA confirmed that visual impoverishment had a significant effect on the subjective rating [$F(6, 90) = 55.6$; $p < .001$, $\eta_p^2 = .77$]. A post hoc pairwise analysis indicated that the first four visual conditions (0–50 %) did not differ from each other but differed significantly almost systematically from the other three visual conditions (66–100 %) (see Table 1). The 66 and 84 % conditions did not differ from each other but both differed significantly from the 100 % condition.

Since the occurrence of illusion differed from one condition to another, we performed a supplementary analysis to ensure that the reduction in the perceived speed of the mirror illusion was not solely due to mixing trials in which

Table 2 Subjective rating and onset for each "visual impoverishment condition" (0, 16, 33, 50, 66, 84 and 100 %) for the nine participants experiencing illusions in each of the seven visual conditions

	0 %	16 %	33 %	50 %	66 %	84 %	100 %
Mean subjective speed (SD)	8.17 (1.40)	7.42 (1.25)	7.19 (1.19)	7.25 (1.95)	6.58 (1.67)	5.19 (1.48)	1.94 (0.78)
Mean onset in seconds (SD)	1.84 (0.99)	1.97 (1.13)	1.82 (1.07)	1.95 (1.08)	2.10 (0.95)	2.57 (1.31)	4.21 (1.40)

For mean onset, only trials in which an illusion occurred were considered (since no onset could be estimated in the absence of illusion)

** $p < .01$; * $p < .05$, *ns* not significant

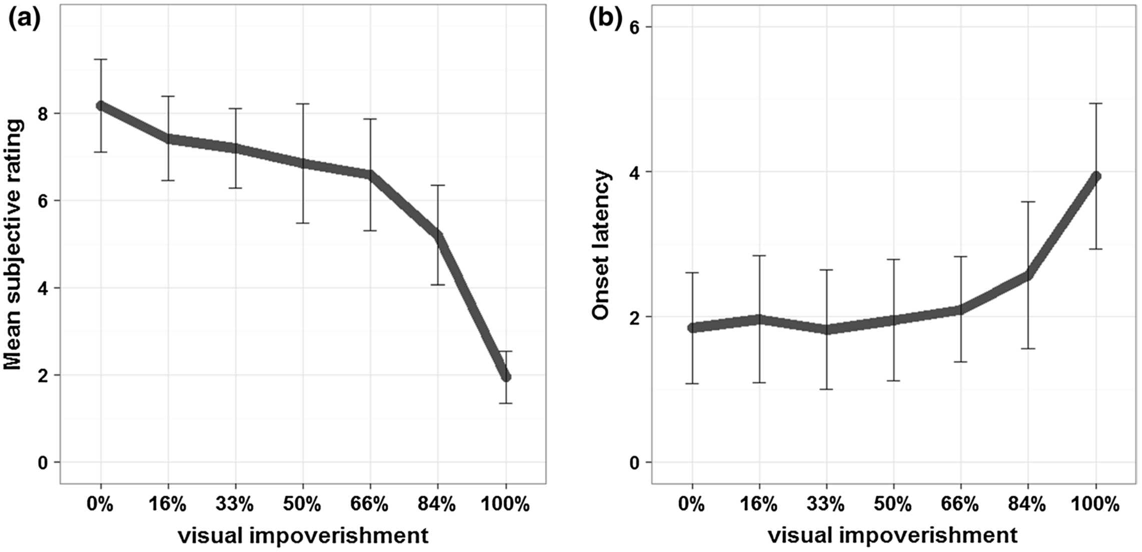

Fig. 4 Mean subjective speed (**a**) and onset latency (**b**) of the kinaesthetic illusion, as a function of the degree of visual impoverishment in the nine participants that experienced illusory displacement in each visual impoverishment condition. The *error bars* correspond to 95 % CIs

illusion occurred and trials in which illusion did not occur (with a subjective rating of 0 in the latter cases, the number of which increased with the degree of visual degradation). We thus 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 visual conditions could not be included in the analysis. This additional ANOVA (involving 9 of the 16 participants) confirmed the effect of visual impoverishment on the speed of illusory movement [$F(6, 48) = 41.3$; $p < .001$, $\eta_p^2 = .83$] (Table 2; Fig. 4a). This analysis based only on trials in which an illusion occurred confirmed that the velocity of the mirror illusion decreases with visual impoverishment.

The latency of illusory movement onset

Only trials in which an illusion occurred could be considered in the latency analysis, and so only the 9 (out of 16) participants who experienced illusory displacement in all seven visual conditions were included in the statistical analysis. The ANOVA revealed a significant effect of visual impoverishment on the latency of illusory movement onset [$F(6, 48) = 23.4$; $p < .001$, $\eta_p^2 = .74$]. Post hoc analysis revealed that the latency of illusory movement onset was significantly longer in the 100 % visual impoverishment condition (4.2 s ± 1.4) than in the other six conditions (see Table 2). However, no difference occurred between the other six visual conditions, from 0 to 84 % conditions (see Fig. 4b).

Experiment 2

Occurrence of the mirror illusion

Among 18 individuals who consented to participate, 15 experienced mirror illusion in the pretest phase and were therefore included in Experiment 2. In those 15 participants, reflection of the passively moving left arm in the mirror evoked a kinaesthetic illusion in the right arm in 92 % of the trials under both flexion and extension conditions (though in the opposite direction) when no masking

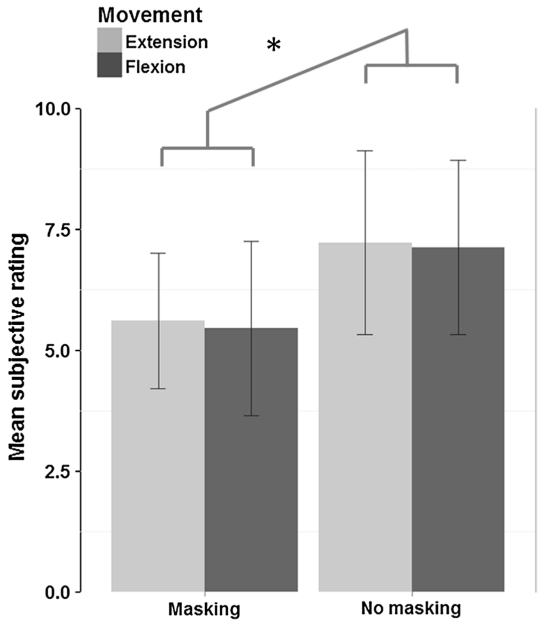

Fig. 5 Mean subjective speed ($n = 15$) of the kinaesthetic illusion, as a function of movement (extension vs. flexion) and proprioceptive masking (masking vs. no masking). The *error bars* correspond to the 95 % CIs. $^*p < .05$

was applied. When proprioceptive masking was applied to the moving arm, the illusion occurrence rate fell slightly (to 83 and 90 % in the extension and flexion conditions, respectively). Statistical analysis indicated that the occurrence rate did not differ when comparing the four experimental conditions ($p > .05$). Few illusory displacements of the unseen right arm occurred in sham trials that lacked reflection of the left arm (i.e. no mirror and no masking), with rates of 18 and 23 % for trials with the extension and flexion movements, respectively.

The speed of illusory movement (subjective rating)

As can be seen in Fig. 5a, the mean ± SD subjective rating of illusory movement was lower when proprioceptive masking was applied to the passively moved left arm (5.52 ± 3.5) than in the absence of masking (7.21 ± 2.7) [$F(1,14) = 4.3$; $p = .05$, $\eta_p^2 = .23$]. In contrast, there was no main effect of the direction of the movement [$F(1,14) < 1$; $p > .05$, $\eta_p^2 = .0006$]. Indeed, when the data from the two masking conditions were pooled, the mean ± SD subjective rating of illusory movement in the extension condition (6.4 ± 3.3) was similar to that reported in the flexion condition (6.3 ± 3.5). The ANOVA showed no significant main effect of the movement (direction) factor [$F(1,14) < 1$; $p = .92$, $\eta_p^2 = .00012$] nor any interaction with the masking factor [$F(1,14) < 1$; $p = .84$, $\eta_p^2 = .0002$].

The latency of illusory movement onset

Only trials in which an illusion occurred could be considered in the latency analysis, and so, only the 10 (out of 15) participants who either experienced illusory displacement in the four experimental conditions or did not forget to indicate the onset of the illusion were included in the statistical analysis. The latency of illusion onset was longer in the masking condition (2.86 ± 1.35 s) than in the absence of masking (2.43 ± 1.21 s), though this effect was not statistically significant [$F(1,9) = 2.9$; $p = .1$, $\eta_p^2 = .24$]. An ANOVA revealed that movement did not have a significant main effect [$F(1,9) < 1$; $p = .41$, $\eta_p^2 = .01$] or a significant interaction with masking [$F(1,9) < 1$; $p = .78$, $\eta_p^2 = .001$]. The latency of illusion onset was therefore similar in the extension and flexion movement conditions.

Discussion

Limited vision of the arm provides sufficient kinaesthetic cues in the mirror illusion

Reflection of the passively moving left arm in the mirror evoked in most individuals a kinaesthetic illusion of right arm displacement in the same direction. The results of Experiment 1 revealed that the occurrence, latency and speed of the mirror illusion were not greatly influenced by visual impoverishment (except under extreme conditions). In fact, the occurrence and latency of the illusion were similar in 0 % to the 84 % conditions, whereas the speed of mirror illusion was only slightly lower under the most extreme visual impoverishment conditions (66 and 84 %). Giving only 16 % vision of the mirror (84 % impoverishment) increased the illusion occurrence from 40 % (no mirror feedback) to ~90 %, rating speed from less than 1–4.5°/s, and reduced onset from 4.2 to 2.5 s. All these effects are large, clearly significant, and bigger than any other of the visual steps. These results attest of the great role of visual cues in the occurrence of mirror illusion in particular and in kinaesthesia in general. They also indicate that even a limited amount of visual information is enough to provide cues for kinaesthetic purposes. These results are in line with a large body of literature data, showing that a limited amount of visual information can provide a high amount of information on biological motion (Johansson 1973). For instance, the kinematics of point-light animations (moving dots that reflect the motion of some key points on a moving body) can reveal many details about the action itself (such as the weight of a box being lifted (Runeson and Frykholm 1981) or how far an object will be thrown (Munzert et al. 2010; for a review, see Troje 2012). What holds true for motion recognition (i.e. the recognition of external actions) might well hold true for the perception of self-motion in general and kinaesthesia in particular. Our results suggest that healthy individuals can easily make out their body segments—even when the visual stimulus is markedly degraded (i.e. a low proportion of "mirror pixels" reflecting parts of the left arm)—and integrate these visual cues to yield a unified perception of arm movement. The rules that govern the use of visual cues for the perception of self-motion might therefore be similar to those governing the perception of the motion of external objects.

Our results attest that a limited amount of visual information is enough to provide many cues for kinaesthetic purposes. In the same vein, it has been shown that a limited morphological matching between the reflected arm and the hidden one is although sufficient as long as position sense is concerned. Holmes et al. (2004) reported that a discrepancy between the visual-mirror feedback about the right arm position and its actual position has a profound effect on reaching performances with the hidden hand. Interestingly, the visual capture of arm position still happens when the reflection of the left arm is replaced by a rubber hand and even block of wood reflection (Holmes et al. 2006). Overall, these data, including those of Experiment 1, confirm that the amount of visual information sufficient to bias the kinaesthetic and position perception of the hidden arm is quite low both in terms of quality (morphological visual matching is not required) and in terms of quantity (only 16 % of the mirror surface is needed for the illusion to arise).

Kinaesthetic sensing of one arm is influenced by somaesthetic stimulation of the other arm

In Experiment 1, some participants reported sensations of right arm displacement when the mirror was completely covered with black pixels (100 % condition) and in the "eyes closed" sham condition, i.e. conditions in which participants did not have any mirror feedback. However, these two conditions were associated with a markedly lower occurrence rate, lower velocity and longer latency, relative to conditions with at least some visual information. Nevertheless, the slight, occasional, illusory displacements observed in the 100 % degradation and "eyes closed" conditions are unquestionably of somaesthetic origin and not of visual origin. As reported above, kinaesthesia is derived from both visual and somaesthetic afferents from the perceived segment and somaesthetic afferents from the other arm. In a recent study by Kuehn et al. (2015), the participant's hands (either one hand at a time or both hands together) were moved passively to new positions. The participant's task was to indicate the perceived location of the tip of the index finger of the designated target hand by orienting a laser beam mounted on a cap. It was found that synchronized bimanual movements were associated with a significantly better position sense, relative to unimanual movements. These results are in line with reports by Izumizaki et al. (2010), Hakuta et al. (2014) and Kigawa et al. (2015). Izumizaki et al. (2010) reported that in the absence of vision, passive displacement of one arm alters the speed of the vibration-evoked illusion experienced with the other arm (by ~30 %). They concluded that the sensation of movement is related to the difference between the inputs from each arm, rather than the vibration-induced signal from the reference arm alone. Therefore, stimulating the somaesthetic afferents of one arm by moving it passively influences perception of the movement of the other arm; this might have occurred when no visual information was available in Experiment 1. It is likely that detection of these slight illusory displacements was facilitated by the experimental context, in which participants had become familiar with the detection of illusory displacement.

The mechanism underlying the bimanual integration of proprioceptive afferents (even for the purpose of unimanual perception) has not been characterized but may stem from the natural tendency to perform bimanual movements in everyday activities. According to Perez et al. (2014), the strength of interhemispheric coupling between the sensorimotor cortices is stronger for bimanual movements. However, Formaggio et al. (2013) recently reported that passive displacement of only one arm can induce bilateral activation of the motor loci (i.e. event-related desynchronization). More generally, it has been found that actively performed unimanual 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 more intense 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 and (2) only the non-dominant left arm was moved passively, our experimental conditions may have facilitated the emergence of illusory movement of the contralateral (right) arm.

Is the kinaesthetic mirror illusion a purely visual illusion?

If stimulation of the somaesthetic afferents of one arm is enough to induce kinaesthetic illusions (albeit limited ones) in the other arm, what is the role of those afferents when they are accompanied by congruent visual cues (such as in the mirror paradigm)? In other words, does the illusory displacement induced in the mirror paradigm have a visual origin (as implicitly suggested in the literature) or does it result from the integration of congruent somaesthetic and visual inputs from two arms that often move synchronously (i.e. bimanual coupling) ? This question prompted us to devise Experiment 2, in which somaesthetic afferents of the passively moved arm were masked by synchronous co-vibration of antagonistic muscles (the biceps and triceps) of the left arm. The results showed that masking the somaesthetic afferents of the arm reflected in the mirror was associated with a significantly lower velocity of illusory displacement of the other arm. These findings confirmed our hypothesis whereby the mirror illusion is not a purely visual illusion. In fact, it appears to result from the combination of congruent signals from the two arms: the visual afferents related to the virtually moving arm and the somaesthetic afferents of the contralateral arm. It must also be borne in mind that masking the afferent signals from the antagonistic muscles of the arm subjected to the illusion has exactly the opposite effect; the mirror illusion occurred earlier (with reduced latency) and more intensely (with a higher perceived speed) than in the absence of proprioceptive masking (Guerraz et al. 2012). Similarly, Metral et al. (2015) showed that a larger degree of spatial incongruence between the mirror arm and the somaesthetically specified position of the unseen arm subjected to mirror illusion (with a shift of between 0° and 90° in the sagittal plane) was associated with a less intense kinaesthetic illusion. Finally, the illusory displacement can be either strengthened or weakened by adding proprioceptive inputs through vibration of the antagonist or agonist muscles of the hidden arm, respectively (Guerraz et al. 2012; Tsuge et al. 2012). Taken as a whole, our results show that somaesthetic cues from both arms exerted an influence on spatial coding of arm position; this influence may inhibit or facilitate the illusion evoked by visual manipulation.

Conclusion

The first major finding of the present experiments is that the marked impoverishment of mirror feedback has only a marginal impact on the use of visual cues for kinaesthesia. This study shows that (as observed for biological motion) a limited amount of visual information may be enough to provide cues for kinaesthetic illusions. Secondly, it appears that the kinaesthetic mirror illusion is not a purely visual phenomenon; it corresponds to the integration of mirror feedback with somaesthetic afferents and results in perceptual facilitation of the contralateral arm what is in line with recent studies of the bilateral integration of proprioceptive information.

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Compliance with ethical standards

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

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