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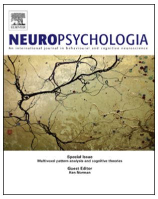

Bimanual coordination with three hands: Is the mirror hand of any help?

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ABSTRACT

The mirror paradigm has been used extensively both as a research tool for studying kinesthesia in healthy individuals and as a therapeutic tool for improving recovery and/or alleviating symptoms in patients. The present study of healthy participants assessed the contribution of the mirror paradigm to motor control in a bimanual coordination task performed under sensorimotor disturbance conditions. In Experiment 1, the participants were required to produce symmetrical circles with both hands/arms at the same time. In Experiment 2, the task consisted of synchronous extension-flexion movements of both arms in the sagittal plane. These tasks were performed under four different visual conditions: (i) mirror vision (i.e. with the non-dominant arm reflected in a mirror – the third hand – and the dominant arm hidden), (ii) full vision (i.e. both arms visible), (iii) with only the non-dominant arm visible and (iv) with the eyes closed. In Experiments 1 and 2, sensorimotor disturbance was applied to the participant's dominant arm by co-vibrating antagonistic muscles (the biceps and the triceps). In the complex circle drawing task, bimanual performance was better in the mirror condition than when participants saw their non-dominant arm only. However, motor performance in the mirror vision condition was little better than in the eyes closed condition, regardless of whether or not sensorimotor disturbance was applied. In Experiment 2, there were no differences between the "eyes closed" and "mirror vision" conditions. Although mirror reflection of one arm has been shown to induce consistent, vivid, perceptual illusions (kinesthetic illusion), our results suggest that it is less effective in modulating motor behavior.

1. Introduction

Over the last two decades, the mirror paradigm has been used extensively to investigate the role of visual afferents in position sense and kinesthesia in healthy individuals. It has also been considered as tool for restoring brain functions in general (Ramachandran & Althschuler, 2009; Rosen & Lundborg, 2005; Dohle et al., 2009) and promoting recovery from hemiparesis in particular.

The reflection of one 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. In recent reports, Guerraz et al. (2012) and Metral, Blettery, Bresciani, Luyat, and Guerraz (2013) observed that mirror reflection of a passively moving arm (i.e. moved by a motorized manipulandum) induced consistent, vivid, kinesthetic illusions of movement of the hidden, static, right arm in the direction of mirror displacement. The researchers showed that the impact of visual afferents on the percept was even greater when proprioceptive afferents were degraded (by the application of widespread vibration to the hidden arm) (Guerraz et al., 2012). This is consistent with the reports in which amputees (lacking proprioceptive afferents) experienced illusions of reminiscent hand/arm kinesthesia when viewing movement of the intact limb in a mirror (Ramachandran & Hirstein, 1998).

It has also been suggested that mirror reflection of one hand's movement has also been suggested to influence motor output of that hidden hand in bimanual tasks (Altschuler, 2005; Franz & Packman, 2004). Franz and Packman (2004) investigated the effect of mirror reflection of circle drawing movements of one hand on the motor output of the other hand. When only one hand was visible, the visible hand drew larger circles (i.e. circles with a larger radius) than the hidden hand. When a total of two hands were visible (either the right and left hand together or the right hand and its reflection in the mirror), there was no longer difference in radius between the hands.

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Franz and Packman (2004) suggested that the visual symmetry of apparent bimanual movement in the mirror condition enhanced spatial coupling of the two hands in a manner similar to actual vision of both hands. However, bimanual coupling is also dependent on paying attention on one hand or the other (Franz, 2004; Buckingham, Main, & Carey, 2011; Peters, 1981). In this respect, mirror vision might well enhance spatial coupling because of attentional symmetry between the two hands (rather than visual symmetry). To better understand the mechanisms underlying mirror facilitation, we decided to investigate bimanual coordination in healthy individuals and under several conditions: mirror vision, actual (non-mirror) vision of both hands, vision of one hand only and in the absence of vision (i.e. an "eyes closed" condition, which was not investigated in previous reports). The eyes closed condition is of particular interest since (in contrast to conditions in which only one hand is visible), spatial attention is probably focused on both hands. In the above mentioned studies, the impact of various visual conditions was evaluated in the absence of experimental disturbances (even though the mirror paradigm is widely used in clinical therapy). We reasoned that the role of visual afferents on bimanual performance might be even more crucial during sensorimotor disturbance. However, one might expect better coordination with full vision by virtue of direct (online) visual corrections that are absent in the mirror condition. In this respect, we evaluated the effect of visually symmetrical (i.e. mirror-reflected) bimanual movement when proprioceptive afferents of the dominant arm were deliberately degraded. This was achieved by simultaneously vibrating antagonistic arm muscles (the biceps and the triceps). As with deafferentation (Rothwell et al., 1982; Teasdale et al., 1993), this method substantially decreases the sensitivity of position perception (Roll, Vedel & Ribot, 1989; Bock, Pipereit, & Mierau, 2007) and alters the subject's ability to perform coordinated visuomotor tasks (Ribot, Roll, & Gauthier, 1986, Gilhodes, Roll, & Tardy-Gervet, 1986) and bimanual coupling (Swinnen et al., 2003). In our first experiment (referred to henceforth as Experiment 1), the bimanual task consisted of describing self-paced circles with both hands simultaneously in a symmetrical mode (i.e. with the left hand moving clockwise and the right hand moving counterclockwise (CCW)) and in the absence of a template. In half of the trials, the dominant arm was vibrated (the sensorimotor disturbance condition). Experiment 2 was similar to Experiment 1, except that the bimanual task consisted of synchronous, self-paced arm extension-flexion in the sagittal plane. From a motor point of view, the task in Experiment 2 was easier (Bangert, Reuter-Lorenz, Walsh, Schachter, & Seidler, 2010) because it involved only one joint for each arm and thus rotation about a single axis only. We reasoned that when compared with Experiment 1's relatively complex drawing task, Experiment 2 might be more sensitive to mirror vision and might reveal different effects.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Thirteen right-handed participants (8 females and 5 males; mean age: 22.1; handedness determined in the Edinburgh Inventory Test (Oldfield, 1971)) took part in Experiment 1. None had a history of visual, proprioceptive or neuromuscular disease. The experiment was performed in accordance with the tenets of the Declaration of Helsinki and the study protocol had been approved by the local independent ethics committee at the University of Savoie (Chambery, France).

2.1.2. Material

Participants sat in front of a large, custom-built box. An open frame (measuring 65 by 65 cm) was positioned vertically in the middle of the box and was oriented parallel to the participant's mid-sagittal. Depending on the experimental conditions, either an opaque board (preventing the participant from directly viewing his/her right hand) or a mirror (measuring 65 by 65 cm) with the reflective surface facing towards the participant's left (see Fig. 1) was positioned against the frame.

An electromechanical physiotherapy vibratory apparatus (Innovative Technology, France) was attached to the right biceps and triceps with elastic bands. In preliminary tests, we ensured that co-vibration (at an initial frequency of 80 Hz) did not induce arm displacement per se during flexion or extension. To this end, the participant positioned his/her right forearms at around 45° to the horizontal. If co-vibration provoked arm displacement (indicating an imbalance between the proprioceptive signals from the antagonist muscles (Gilhodes et al., 1986)), the frequency of one of the two vibrators was reduced until equilibrium was obtained (i.e. no arm movement). In Experiment 1, the frequency of the biceps vibrator was reduced to 70 Hz and 60 Hz in two and one participants, respectively, whereas the frequency of the triceps vibrator remained at 80 Hz. Performance was recorded with an electromagnetic motion capture system (FASTRAK™, Polhemus, Colchester, VT). A sensor was positioned on each index finger so that displacements of right and left index fingers in the X and Y axes (i.e. in the horizontal plane) were continuous recorded. In order to avoid wrist movements, participants wore splints on each hand. The data were sampled at a frequency of 60 Hz.

2.1.3. Procedure

The participants sat in front of the mirror box, with their arms positioned on each side of the wooden frame. Participants were required to describe circles of constant radius on a horizontal board by moving both hands continuously, simultaneously in a symmetrical mode and at freely-chosen, comfortable speed. The left hand moved clockwise and the right hand moved CCW. Participants started with their fingers at approximately the 12.00 position on the circle. Although the investigator demonstrated the task prior to the experiment, the horizontal board did not have a circular template and the participants were not given any online feedback on the quality of the circles actually described. Under all visual conditions, the participants were instructed to focus their visual attention on the lower boundary of the central frame (which allowed vision of both hands under the mirror and full vision conditions) and to tilt their head forward and to the left slightly. This ensured that head position was similar in all four visual conditions (Guerraz, Blouin, & Vercher, 2003; Guerraz, Caudron, Thomassin, & Blouin, 2011). The participants were told to stop moving their arms once they had described five circles. In half of the trials, sensorimotor disturbance was initiated immediately before the start of the motor task and was maintained throughout the task. When the task had been completed, the vibrators were switched off and participants were asked to move both arms freely and synchronously for a few seconds (to prevent muscle fatigue). Before data collection, the participants performed a few practice trials in order to familiarize themselves with the experimental conditions.

Four visual conditions were implemented (see Fig. 1): (i) mirror vision: the participant saw his/her left hand and forearm and his/her reflection in the mirror, whereas the right arm was out of sight; (ii) full vision: participants saw the left hand but also the right hand through the open frame; (iii) left hand vision: only the left hand and forearm were visible; (iv) no vision: eyes closed. The visual conditions were paired with two disturbance conditions (no disturbance vs. sensorimotor disturbance) to give a total of 8 experimental conditions in a within-subjects design. Each condition was repeated 4 times in pseudo-random order, yielding a total of 32 trials per participant.

2.1.4. Data analysis

Our analysis was based on that developed by Franz and Packman (2004), in which a continuous phase is computed for trajectories that do not form perfect circles or revolve around a stable center. Each point on a trajectory was individually associated with a figure that subtended exactly 360°. Using the two extremes of a 200 ms moving window, the tangential angle (TA) with respect to 12 o'clock was calculated for each point (n), where $x\mathrm{dif}_n = x_{n+6} - x_{n-6}$ for the difference in displacement along the x axis, $y\mathrm{dif}_n = y_{n+6} - y_{n-6}$ for the difference in displacement along the y axis and $TA_n = \arctan x\mathrm{dif}_n / y\mathrm{dif}_n$.

The instantaneous value for whole-circle variables (such as the period) was calculated by associating each point on the trajectory with a single circle. For each point, the algorithm searches backwards along the TA profile until it finds a start point s_n at which the TA differs from the TA at n by 180°. The algorithm then searches 180° forward to find an endpoint (e_n). The points between s_n and e_n approximate a circle for which the range (s_n to e_n) and period (circle duration) are then evaluated.

The coordinates of the circle's center were determined by taking the values halfway between the upper and lower extremes in the x and y axis, where center $x_n = \mathrm{midpoint}\ [\min(x_{\mathrm{range}}), \max(x_{\mathrm{range}})]$ and center $y_n = \mathrm{midpoint}\ [\min(y_{\mathrm{range}}), \max(y_{\mathrm{range}})]$. Next, the radius was calculated at n by measuring the length of a line drawn from the circle's center to n, where $\mathrm{radius}_n = [(x_n\text{-center } x_n)^2 + (y_n - \text{center } y_n)^2]^{1/2}$. Next, the mean radii for the right and left hand were calculated for the continuous drawing of four circles.

Time-lag: Time-domain coordination was examined by cross-correlating the TAs of the left and right hand circles. To determine whether one hand preceded or followed the other, the time-lag was computed by identifying the location of the peak correlation coefficient. A negative time-lag value indicated that left hand displacement preceded right hand displacement, and vice versa.

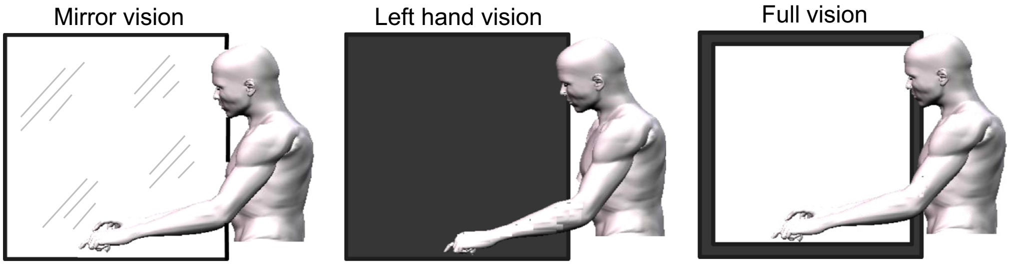

Fig. 1. Visual conditions of experiment 1. In the 'mirror condition' (left), participants can see the left hand and its reflection in the mirror. In the 'left hand vision' condition (middle), an opaque board prevents vision of the right hand. In the 'full vision' condition (right), the participants can see the right hand through the open frame. Eyes closed condition is not depicted.

2.1.5. Statistical analysis

Radius and time lag data were analyzed using $2 \times 4 \times 2$ [hand × vision × disturbance] repeated measures analysis of variance (ANOVAs), in a within-subjects design. For all ANOVAs, the recorded values were Huynh–Feldt-corrected and the partial eta squared (a measure of effect size) was noted. Pairwise post hoc comparisons were performed using the Newman–Keuls method. All analyses were performed with the udsAnova "R" statistical software package (https://sites.google.com/site/udsanova/home). The threshold for statistical significance was set to $p < .05$.

2.2. Results of Experiment 1

2.2.1. Circle size (radius) of left and right hand circles

2.2.1.1. Circle size (radius) in the absence of sensorimotor disturbance. In the absence of sensorimotor disturbance (Fig. 3A), the circles described by the left and right hands had similar radii (except in the left hand vision condition, in which right hand circles were smaller than left hand circles; pairwise post-hoc test, $p = .0001$). When the two hands were out of sight (i.e. no vision), the circles described by the left and right hands had smaller radii than under vision conditions but did not differ from each other ($p = .24$). Hence, bimanual coordination was maintained in the no vision condition (Fig. 3C).

2.2.1.2. Circle size (radius) in the presence of sensorimotor disturbance. When sensorimotor disturbance was applied to the right arm, the right hand circles were smaller than the left hand circles (by between 9% and 25%, depending on the visual condition (Fig. 2)). A contrast analysis indicated that this worsening in bimanual coordination was less pronounced in the full vision condition (9.2%) than in the no vision condition (15.5%) and the mirror vision (16.3%) condition (both $p < .05$). The latter two conditions did not differ significantly ($F(1,12) = 1.3$, $p = .27$). The percentage reduction in the latter two visual conditions was smaller than when only the left hand was visible (24.5%) ($p < .05$). For the sake of clarity, left hand–right hand differences are reported in Fig. 3C.

2.2.2. Time lag between the left and right arms

When all visual conditions were collapsed, the phase changed from leading with the left hand in the control condition towards leading with the right hand during sensorimotor disturbance (a main effect of disturbance: $F(1,12) = 6.6$ $p = .024$, $\eta_p^2 = .35$). However, this effect was limited (14 ms on average), and post-hoc analysis revealed that the difference was not statistically significant under any of the four visual conditions (p-values $> .06$ in all cases). The ANOVA also revealed a significant effect of vision ($F(3,36) = 5.6$ $p < .003$, $\eta_p^2 = .31$); with a significant (left-hand) phase lead when only the left hand was visible (50 ms) and to a lesser extent in the eyes closed condition (34 ms). The interaction between vision and disturbance was not statistically significant ($F(3,36) = .68$ $p = .56$, $\eta_p^2 = .06$).

2.2.3. The orientation of ellipse-like drawings

As can be seen in Fig. 2, the hand motions were elliptical rather than perfectly circular. There were clockwise and CCW tilts of the principal axis for the right and left hand respectively. In an additional analysis, we assessed the impact of experimental manipulation on the orientation of the major diameter (i.e. the principal axis) of motor productions. In the absence of disturbance, the orientation of the ellipse's principal axis (averaged across all visual conditions) was 47° clockwise for the right hand and 32° CCW for the left hand (Fig. 4). During sensorimotor disturbance, the principal axis of the ellipses moved towards a 12 o'clock position for both hands but the effect was greater for the vibrated hand (evidencing a hand × disturbance interaction: $F(1,12) = 15.6$ $p < .002$, $\eta_p^2 = .56$). Post hoc analysis revealed that this effect achieved statistical significance ($p < .05$) for the vibrated arm only. Although the effect was less pronounced for full vision than for the other visual conditions, vision was associated with neither a significant main effect ($F(3,36) = 2.4$, $p = .08$, $\eta_p^2 = .28$) nor a significant interaction with hand or disturbance ($F(3,36) = 1.8$, $p = .15$, $\eta_p^2 = .13$).

2.3. Discussion of Experiment 1

The present results confirm an earlier observation of more efficient bimanual coupling under full vision or mirror vision conditions (relative to vision of one hand alone) (Franz & Packman, 2004). However, our results also revealed that there were only slight differences in bimanual coordination between the mirror vision and eyes closed conditions, regardless of whether or not sensorimotor disturbance was applied. Indeed, in the absence of sensorimotor disturbance, size differences between circles described with the left and right hands were only observed when the left hand was hidden. The eyes closed condition was associated with the lowest radii, as already reported by Zelaznik and Lantero (1996) for one-handed (non-coordinated) circle drawing. However, the radii decreased to the same extent for left and right hand circles and bimanual coordination was maintained.

When sensorimotor disturbance was applied to the right arm, right hand circles shrunk and marked left–right differences were therefore observed under all visual conditions. The reduction in circle size in response to vibration confirms an earlier observation (Verschuren, Swinnen, Cordo, & Dounskaia, 1999). However, bimanual coordination was less affected by sensorimotor disturbance in full vision conditions than in mirror vision and no vision conditions, which in turn were less affected than the fourth condition in which only the left hand was visible. The decrement in bimanual coordination associated with of sensorimotor disturbance was similar in the mirror and no-vision conditions. As reported previously, the participants described ellipses rather than perfect circles (Franz, Rowse, & Ballantine, 2002). The longest axis was between 12 and 3 o'clock for right hand circles and between 9 and 12 o'clock for left hand circles. Our results revealed that under all visual conditions, sensorimotor disturbance was associated with a significant mean

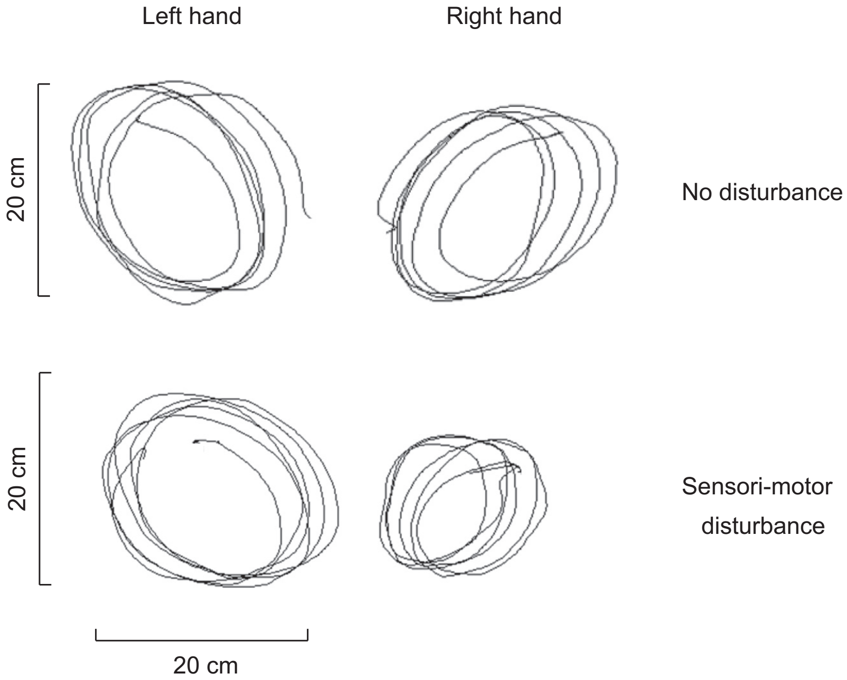

Fig. 2. Representative bimanual circle drawing in control (no disturbance—upper panel) and sensorimotor disturbance conditions applied to the right arm (lower panel) in the mirror condition. With sensorimotor disturbance, the radius of the circle drawn by the right hand is reduced.

CCW shift in the ellipse's long axis. Although our observation of an effect of sensorimotor disturbance is not surprising per se, a systematic CCW shift of drawing orientation is rather curious. This might have been caused by vibration imbalance during motor production. Although we checked that co-vibration did not induce arm displacement (either in flexion or extension) in a static position, we cannot be sure that this equilibrium was obtained during motor production. Indeed, it has been shown that the impact of vibration on illusory arm displacement or motor production depends on muscle contraction and length (Goodwin, McCloskey, & Mattews, 1972; Capaday & Cooke 1981, 1983), which of course vary during a drawing task.

Given the absence of a clear difference between mirror vision and no vision, we performed Experiment 2. This bimanual task consisted of synchronous, self-paced arm extension-flexion in the sagittal plane. The objective was to establish whether mirror reflection would be more helpful in an easier motor task that involved (i) only one joint for each arm and (ii) rotation about a single axis (the sagittal axis).

3. Experiment 2

3.1. Methods

3.1.1. Participants

Ten right-handed participants (7 females and 3 males; mean age: 23.9) took part in Experiment 2. None had a history of visual, proprioceptive or neuromuscular disease.

3.1.2. Material

The material was similar to that used in Experiment 1. Performances were recorded with the electromagnetic motion capture system, with sensors mounted on each splint at the wrist. The data were sampled at a frequency of 60 Hz.

3.1.3. Procedure

The procedure was similar to that of Experiment 1, except that the motor task consisted of arm extension-flexion. Before starting the trial, participants sat in front of the mirror box with their forearms positioned horizontally. They were then required to synchronously extend and flex their arms in the sagittal plane and at a comfortable, freely-chosen speed. The participants were told not to touch the horizontal base of the box or their shoulders. Once five extension-flexion movements had been performed, the investigator told the participants to stop. As in Experiment 1, the four visual conditions (mirror vision, full vision, left hand vision and no vision) were matched with two disturbance conditions (no disturbance and sensorimotor disturbance), giving a total of eight experimental conditions in a within-subjects design. Each condition was repeated four times in pseudo-random order, yielding a total of 32 trials per participant.

3.1.4. Data analysis

3.1.4.1. Amplitude of arm movements. The amplitude of each sub-movement (i.e. flexion and extension, separately) was calculated as the peak-to-peak arm anteroposterior displacement in the sagittal plane (measured in degrees). For each trial, the results of eight sub-movements were averaged.

Time-lag: The extent of time-domain coordination between the arms was examined by cross-correlating the respective angular displacements.

3.1.5. Statistical analysis

Movement amplitude and time lag were analyzed using a $2\times4\times2$ [hand $\times$ vision $\times$ disturbance] repeated measures ANOVA in a within-subjects design. For all ANOVAs, the recorded values were Huynh–Feldt-corrected and the partial eta squared was noted. Pairwise post hoc tests were performed using the Newman–Keuls method. The threshold for statistical significance was set to $p<.05$.

3.2. Results

3.2.1. Amplitude of arm movements in the absence of sensorimotor disturbance

In the absence of sensorimotor disturbance and under all visual conditions (Fig. 6A), the amplitude of right arm movements was slightly larger (by $\sim3^\circ$, on average) than that of left arm movements (pairwise tests: $ps<.05$) (Fig. 5). This left–right difference was similar under all four visual conditions (contrast analysis: $ps>.05$). As observed in the circle drawing task in Experiment 1, both left and right arm movements tended to be less ample in eyes closed condition. Left hand–right hand differences are reported in Fig. 6C.

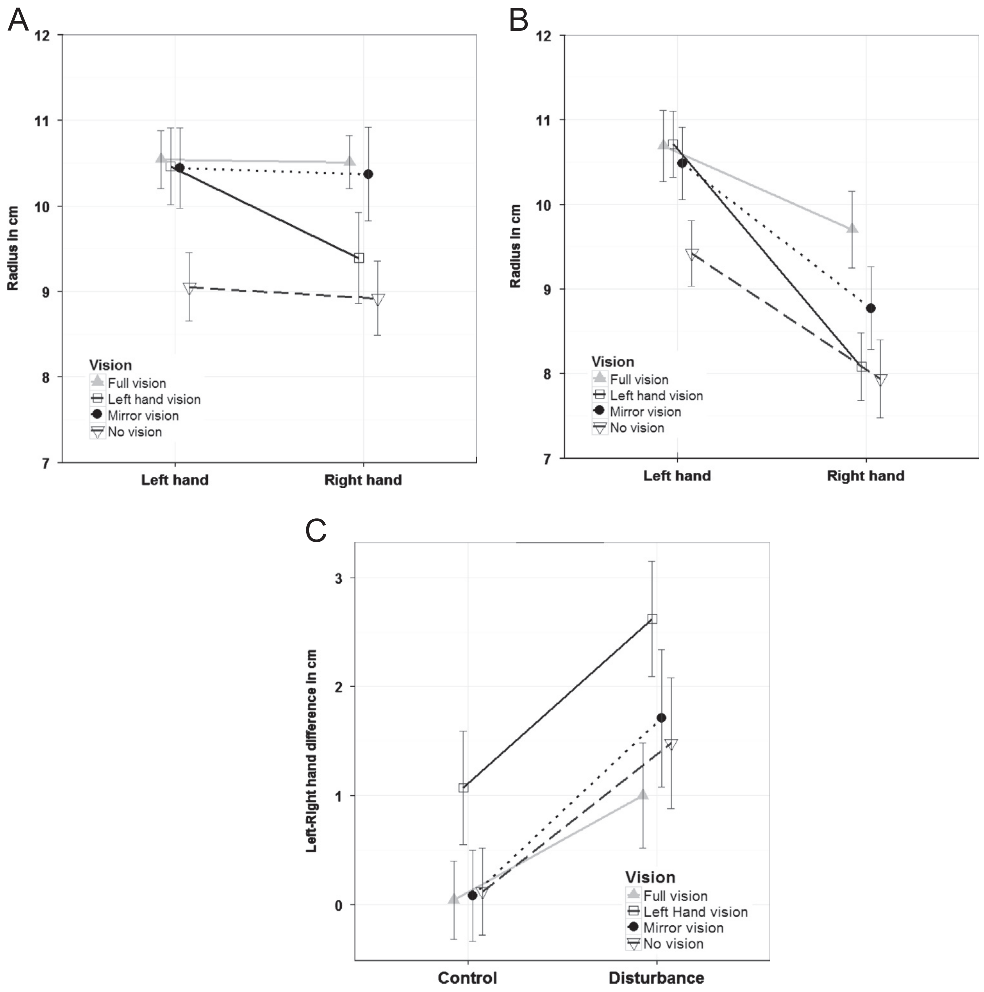

Fig. 3. Mean circle size (radii) for left and right hands and four visual conditions in the control (A) and sensorimotor disturbance (B) conditions. The mean difference between left and right circle radius in the four visual conditions is depicted in C. A positive value indicates that the left hand circle radius was greater than the right hand one. Error bars represent confidence interval.

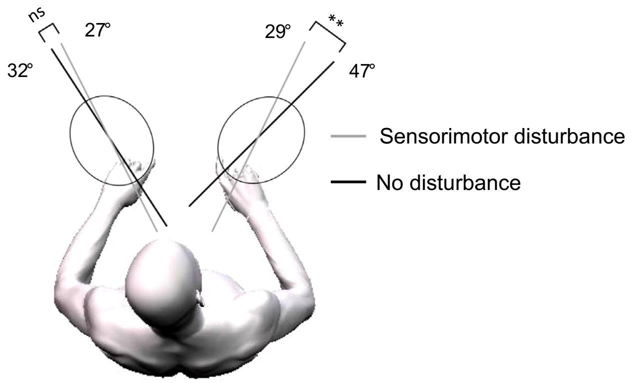

Fig. 4. Representation of the mean principal axis for the right and left hands drawings in the control and disturbance conditions.

3.2.2. Amplitude of arm movements in the presence of sensorimotor disturbance

In the presence of sensorimotor disturbance (Fig. 6B), the angular amplitude of right arm movements was significantly lower than that of the left arm under all four visual conditions (post hoc test: $p<.05$) (Fig. 6). However, the difference between right and left arm movements was smaller in the full vision condition ($m=5.6^{\circ}$) than in the other three visual conditions (no vision: $m=8.5^{\circ}$; mirror vision: $m=9.8^{\circ}$; left hand vision: $m=10.4^{\circ}$). This finding was confirmed in contrast analysis (full vision vs. no vision: $p=.05$; full vision vs. mirror vision: $p=.03$; full vision vs. left hand vision: $p=.02$). Contrast analysis also revealed that the difference between right and left arm movements in the presence of sensorimotor disturbance was similar in the no vision, mirror vision and left hand vision conditions (mirror vision vs. left hand vision: $p=.37$; mirror vision vs. no vision: $p=.48$; no vision vs. left hand vision: $p=.73$). Left hand–right hand differences are reported in Fig. 6C.

3.2.3. Time lag between left and right arms

No significant phase lags between right and left hand displacements were observed in any of the visual/disturbance conditions. An ANOVA confirmed the absence of significant main effects of vision ($F(3.27)=1.06$ $p=.38$) and disturbance ($F(1.9)=.76$; $p=.41$) and the absence of a significant interaction between the two factors ($F(3.27)=.49$; $p=.69$).

3.3. Discussion of Experiment 2

In Experiment 2, the bimanual task consisted of synchronous, self-paced arm extension-flexion in the sagittal plane. Our results revealed that in the absence of sensorimotor disturbance, right arm movements were more ample than left arm movements. One can hypothesize that this difference is related to the participant's

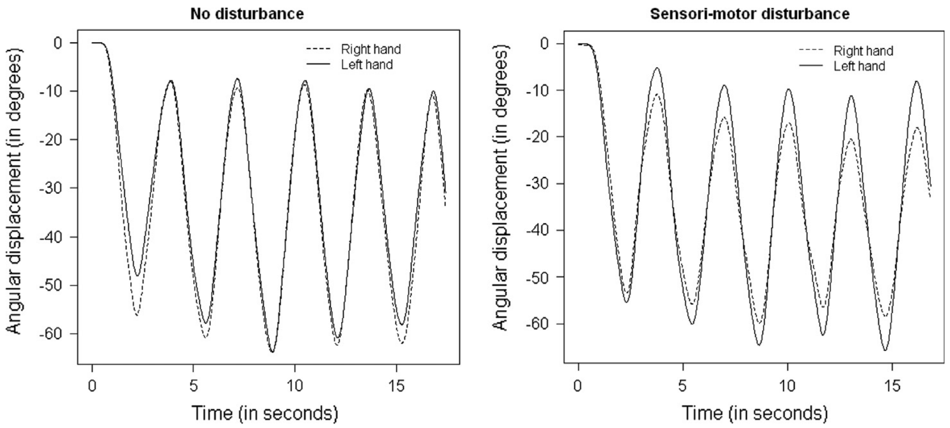

Fig. 5. Representative bimanual flexion-extension trials under control and sensorimotor disturbance conditions. The trials depicted were performed in the eyes closed condition. Overall, the mean angular excursion collapsed across all visual and disturbance conditions and the two hands was 53.3° for a mean duration of 1.71 s per sub-movement.

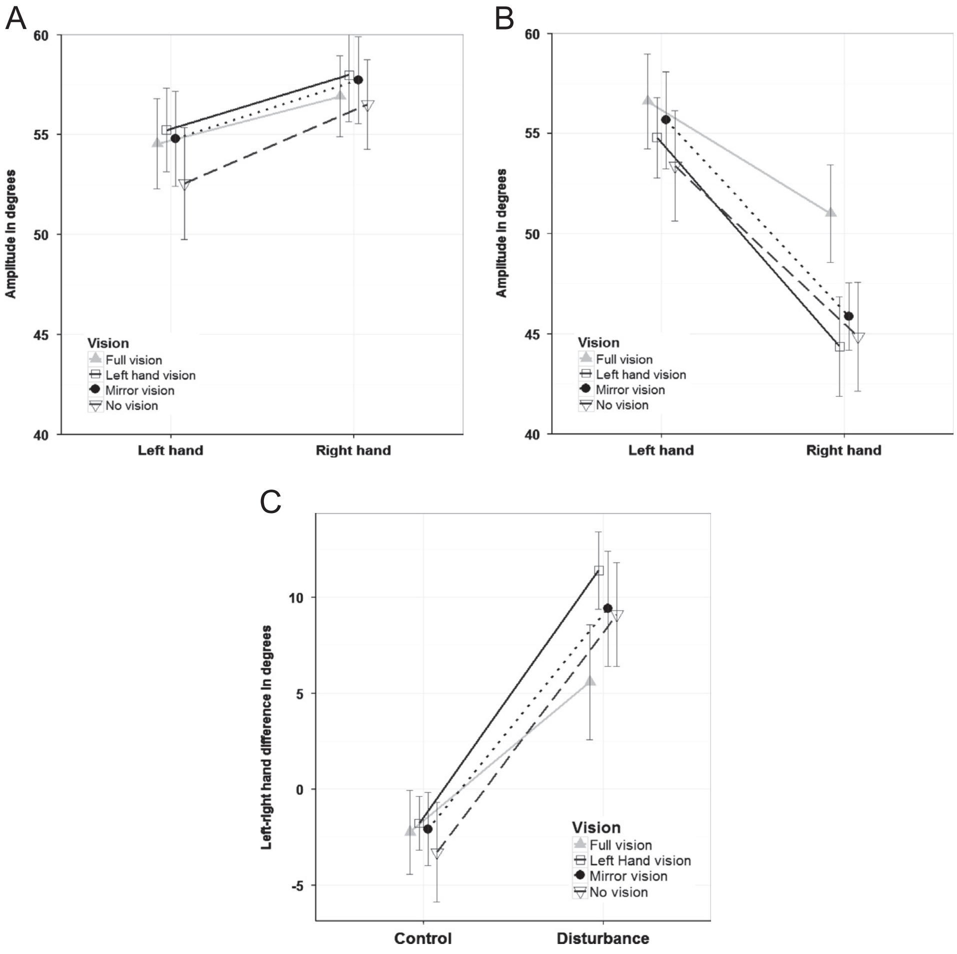

Fig. 6. Mean angular amplitude (in degrees) of left and right arms in the four visual conditions and in the control (A) and sensorimotor disturbance (B) conditions. The lower panel (C) depicts the mean difference between left and right excursion in the four visual conditions. A positive value indicates that the left arm angular excursion was larger than the right arm excursion. Error bars represent confidence interval.

head position during the experiment (slightly tilted leftward and forward). Although head tilt is well known to affect hand/arm motor action (Guerraz et al., 2003), other explanations are credible. Given that the head was slightly tilted forward, the participant might have made smaller left arm movements on order to avoid hitting his/her face (i.e. by allowing a safety margin).

In contrast to Experiment 1, we did not observe a clear effect of the visual condition on bimanual coordination (i.e. left–right differences) in the absence of sensorimotor disturbance. When sensorimotor disturbance was applied, it had less impact on bimanual coordination and/ motor performance in the full vision condition than in the other visual conditions. As was found for Experiment 1, there were no significant differences between mirror vision and no vision conditions.

4. General discussion

The present results confirm earlier observations of complex movements (such as circle drawing) for which bimanual coupling is more effective under full vision or mirror vision conditions than when only one hand is visible. Indeed, the results of Experiment 1 showed that in the absence of sensorimotor disturbance and when participants saw only one hand (the left hand), the circle size produced by the hidden hand (i.e. the right hand) was smaller than that of the seen hand. This difference was not observed under full vision or "mirror facilitation" conditions. This phenomenon has already been reported for both the left and the right hands by Franz and Packman (2004). When sensorimotor disturbance was applied to the hidden arm, a similar difference between the left and right hands was observed for all visual conditions. However, the largest difference in bimanual coupling still occurred when only one hand was visible.

The results of Experiments 1 and 2 also revealed that bimanual coupling was less affected by sensorimotor disturbance in full vision than in mirror vision. For the bimanual circle drawing task, we were surprised to find that there was no difference in motor performance between the mirror vision and the eyes closed conditions (and regardless of whether or not sensorimotor disturbance was applied). Based on the absence of difference between these two visual conditions, we performed Experiment 2—a bimanual task in which both arms were synchronously moved in self-paced extension-flexion in the sagittal plane. The purpose was to investigate whether mirror reflection would be more helpful in this relatively easy motor task (which involved only one joint for each arm and rotations about the sagittal plane only). As in Experiment 1, we did not find any difference between the mirror vision and the eyes closed conditions. This conclusion could not have been drawn in earlier studies in which mirror vision was compared with full vision and vision of one hand only but never with an eyes closed condition.

The fact that coordination was better with full vision than with mirror vision in the presence of sensorimotor disturbance (and in both Experiments 1 and 2) is not particularly surprising. Indeed, when participants can see their two hands (full vision), visual feedback can be used directly to compare the amplitude of motion of the two arms. Online corrections can therefore limit the impact of the disturbance (Reynolds & Day, 2012; Day & Lyon, 2000). In contrast, when visual information about the right arm actually consists of the mirror reflection of the left arm, visual correction of the right arm's trajectory is impossible because trajectory errors cannot be visually detected (as in the eyes closed condition).

Furthermore, the fact that mirror vision and no vision conditions generated the same pattern of results in the circle drawing task (i.e. better coordination than with vision of one hand only) raises the question of which processes are at work under these various visual conditions. It has been hypothesized that the symmetry of apparent bimanual movement in mirror vision enhances spatial coupling of the two hands in a manner similar to that produced by actual vision (Franz & Packman, 2004). It has further been suggested that the mirror neuron system (Buccino, Solodkin, & Small, 2006; Filimon, Nelson, Hagler, & Sereno, 2007; Ramachandran & Althschuler, 2009) is involved in mirror facilitation (Franz & Packman, 2004; Ramachandran & Altschuler, 2009). The mirror neurons may provide a direct interface between the action viewed and the action produced. Although this hypothesis is relevant in some cases, it cannot account for the pattern of results observed here (i.e. better bimanual coupling in the absence of vision than with vision of one hand only, and the similar coupling in the absence of vision and with mirror vision). Furthermore, several recent electrophysiological studies (Praamastra, Torney, Rawle, & Miall, 2011, Funase, Tabira, Higashi, Liang, & Kasai, 2007) and functional magnetic resonance imaging studies (Fink, Marshall, Frith, Frackowiak, & Dolan, 1999; Michielsen et al., 2011) have failed to demonstrate the mirror neuron system's involvement in the mirror box paradigm. In contrast, Michielsen et al.'s study of stroke patients revealed the activation of brain areas known to be involved in self-awareness and spatial attention (the precuneous and posterior cingulate cortex). Similar results have previously been reported in healthy subjects (Fink et al., 1999).

Several researchers have reported on the effect of attentional asymmetry on bimanual tasks (Franz, 2004; Buckingham et al., 2011; Peters, 1981). In his pioneering work, Peters (1981) suggested that attention was divided asymmetrically between the two hands, with the right hand receiving more attentional resources in right-handed people. Consequently, right handers perform worse in a bimanual tapping task when the left hand is assigned a more attentionally demanding portion of the task than the right hand. The decrement in bimanual coupling when only one hand is visible might result from this type of attentional bias towards that hand. On the same lines, providing subjects with a virtual right hand (a third hand!) might divert their attention towards the hidden or proprioceptive hand. This attentional hypothesis might also account for the participant's tendency to change from leading with the left hand in the absence of sensorimotor disturbance to leading with the right hand in the presence of sensorimotor disturbance (as observed in Experiment 1). Indeed, co-vibrating the right arm muscles might partly redirect the focus of attention towards that arm and therefore reduce the asymmetry introduced by the mirror-paradigm set-up. This hypothesis could be tested in experiments in which visual attention is manipulated.

The absence of a difference between the full vision, mirror vision and no vision conditions in Experiments 1 and 2 in the absence of sensorimotor disturbance indicates that bimanual performance is largely mediated by either proprioceptive afferents or efferent signals rather than visual signals. In Experiments 1 and 2, the involvement of muscle proprioceptive afferents was unambiguously evidenced by the large decrease in bimanual performance when the right arm muscles were co-vibrated. On the same lines, Spencer, Ivry, Cattaert, and Semjen (2005) observed circle size in a bimanual drawing task and reported that spatial coupling was clearly degraded in patients who were deprived of somatosensory feedback. The researchers suggested that the integration of somatosensory signals from the two hands is important for fine-tuning and maintaining the movement trajectories. In contrast, these signals appeared to be less important for achieving temporal coupling-indicating that efferent signals from the two limbs may be sufficient to sustain the basic temporal pattern on a cyclic basis (Spencer et al., 2005).

Overall, our results failed to show that mirror vision led to better bimanual motor coordination than the absence of vision. This is consistent with recent reviews that have questioned the benefit of mirror therapy over mental imagery or bimanual coupling in recovery from hemiparesis (see Rothgangel, Braun, Beurskens, Seitz, & Wade, 2011; Moseley, Gallace, & Spence, 2008). However, the mirror paradigm is particularly valuable because it enables us to (i) study the effects of visual afferent inputs on kinesthesia (Guerraz et al., 2012) and (ii) elicit phantom limbs that may not have been sensed for a long time in some amputees (Ramachandran & Hirstein, 1998).

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