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Through the looking-glass: Mirror feedback modulates temporal and spatial aspects of bimanual coordination

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ABSTRACT

Mirror therapy has become an effective and recommended intervention for a range of conditions affecting the upper limb (e.g. hemiparesis following stroke). However, little is known about how mirror feedback affects the control of bimanual movements (as performed during mirror therapy). In this study, in preparation for future clinical investigations, we examined the kinematics of bimanual circle drawing in unimpaired participants both with (Experiment 1) and without (Experiment 2) a visual template to guide movement. In both experiments, 15 unimpaired right-handed participants performed self-paced continuous bimanual circle-drawing movements with a mirror/symmetrical coordination pattern. For the *mirror* condition, vision was directed towards the mirror in order to monitor the reflected limb. In the *no mirror* condition, the direction of vision was unchanged, but the mirror was replaced with an opaque screen. Movements of both hands were recorded using motion capture apparatus. In both experiments, the most striking feature of movements was that the hand *behind the mirror* drifted spatially during the course of individual trials. Participants appeared to be largely unaware of this marked positional change of their *unseen* hand, which was most pronounced when a template to guide movement was visible (Experiment 1). Temporal asynchrony between the limbs was also affected by mirror feedback in both experiments; in the *mirror* condition, illusory vision of the *unseen* hand led to a relative phase lead for that limb. Our data highlight the remarkable impact that the introduction of a simple mirror can have on bimanual coordination. Modulation of spatial and temporal features is consistent with the mirror inducing a rapid and powerful visual illusion, the latter appearing to override proprioceptive signals.

1. Introduction

Mirror visual feedback of movement provides the basis for mirror therapy, an intervention that has become increasingly prevalent over the past 20 years in the management of various conditions such as chronic pain and stroke (Cacchio et al., 2009; Thieme et al., 2018). In the case of stroke, mirror therapy has primarily been used to target resulting hemiparesis of the upper limb; a recent systematic review reported its ability to improve both motor function and motor impairment in this group of patients (Thieme et al., 2018).

The typical arrangement during mirror therapy is as follows. The patient sits with their arms resting on a table with a mirror aligned to their mid-sagittal plane, the reflective side facing towards the unimpaired limb. The patient is then encouraged to make symmetrical

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and synchronous bimanual movements while focusing their visual attention on the reflection of the unimpaired limb in the mirror. The resulting illusion can be rapidly elicited and vivid; as the reflection of the *seen* hand in front of the mirror appears spatially congruent with the felt position of the *unseen* hand behind the mirror, one's experience is of actually viewing the unseen hand. The experience appears strengthened by movement, providing the intended movement and the visual consequences remain congruent (Fink et al., 1999).

Early mirror therapy trials for amputees with phantom limb pain demonstrated the impact of the mirror illusion (Ramachandran et al., 1995; Ramachandran & Rogers-Ramachandran, 1996). When patients placed their 'phantom' behind the mirror, they were able to relieve their discomfort by watching the reflection of the intact arm moving in the position where their phantom limb was located. The visual feedback was found to provide relief from phantom limb pain (Ramachandran et al., 1995). Subsequently, mirror therapy has been applied to other conditions where a single limb is impaired, for example following hemiparetic stroke (Altschuler et al., 1999), and eliciting the illusion has long been regarded as one of the critical elements of mirror therapy (McCabe, 2011).

As referred to above, while mirror therapy training has been found to have significant benefits, understanding how mirror therapy works has proved elusive. At the neural level, there appear to be multiple possibilities. Deconinck et al. (2015) explored three related hypotheses in providing a meta-analysis of published data. Finding little support for the involvement of the *mirror neuron system*, the authors suggest mirror therapy activates a network of brain areas relating to monitoring action and attention. An alternative possibility is that mirror therapy is associated with the activation of the normally inhibited ipsilateral (contra-lesional) motor pathways, thought to play a role more generally in recovery (Schwerin et al., 2008).

At the behavioural level, complexities of the intervention are challenging for researchers as the therapeutic benefits may arise from a number of different sources. For example, research suggests that bimanual movement training (in the absence of a mirror) may also have clinical benefits (Cauraugh et al., 2010), providing the real possibility that it is simply the performance of these movements alone that conveys therapeutic value. Nevertheless, one suggestion that appears worthy of consideration is that mirror visual feedback enhances related bimanual coupling (Guerraz, 2015). To our knowledge, this issue has not been examined in stroke survivors to date, though two studies have addressed the impact of a mirror on bimanual coordination in unimpaired individuals (Franz & Packman, 2004; Metral et al., 2014). Both these studies used a bimanual circle-drawing task and focused on how mirror visual feedback modulated spatial and temporal aspects of bimanual coordination. The most striking feature across both studies was a tendency for more equal circle size (i.e. greater spatial coupling) when the mirror was present in comparison to when it was replaced by an opaque screen. Neither study found a modulatory effect of mirror visual feedback on the small asynchronies that are typically found for the task (Swinnen et al., 1996).

A surprising aspect of these studies was that neither examined any changes that occurred in limb position during trials. Previous studies examining reaching movements with mirror visual feedback highlight that conflict between proprioceptive and visual signals about the position of the unseen limb can lead to significant related errors (Holmes et al., 2004; Holmes & Spence, 2005), with vision dominating perception, particularly in relation to position along the sagittal plane (Snijders et al., 2007). Consistent with these findings, our own informal observations of limb position when making bimanual circle-drawing movements with mirror visual feedback suggested a tendency for the unseen hand to *drift*, particularly along the sagittal plane. These observations together with previous findings, were the motivation for the studies of unimpaired participants reported here.

We initially aimed to replicate the experiment conducted by Franz and Packman (2004) but with some differences. Firstly, the trial length was increased from eight seconds to 15 s; some have argued that the onset of the mirror illusion follows around six seconds of exposure (Holmes et al., 2004; Tajima et al., 2015), and we aimed to provide sufficient time to observe the effects of the illusion. Secondly, a visual template was introduced to provide participants with explicit spatial information about the position and size of the circles to be drawn. Thirdly, while including the same conditions as Franz and Packman (2004), instructions to participants about where to direct their vision were modified. Rather than have participants direct their visual attention to the junction between the table and the mirror, they were encouraged to direct their visual attention to their hand reflected in the mirror. This was done to provide a more authentic representation of how mirror therapy typically proceeds (Ramachandran & Altschuler, 2009; Rothgangel et al., 2011).

The primary hypothesis is related to *positional drift*. In contrast to studies reported by.

Franz and Packman (2004) and Metral et al. (2014), the position of the centre of circles was tracked as trials unfolded. Given our informal observations noted above, along with studies reporting conflicts between vision and proprioception in different tasks using mirror visual feedback (Holmes et al., 2004; Holmes & Spence, 2005; Snijders et al., 2007; Tajima et al., 2015), it was hypothesised that the unseen hand would show positional drift in the *mirror* conditions, driven by illusory visual information. Accordingly, we predicted that as movement commenced in the mirror condition, any deviation with the seen limb (however small) away from the visual template would be perceived as a deviation in the unseen limb (as a result of the visual illusion) and participants would make 'corrective' movements in response with this limb rather than the seen limb. As these movements would not actually correct the source of the perceived error, subsequent movements of the unseen limb within the trial would continue to be adjusted, leading to positional drift of the unseen limb. In addition, circle size and between-limb synchrony were also monitored, consistent with the studies of Franz and Packman (2004) and Metral et al. (2014).

2. Experiment 1 methods

2.1. Participants

The participants were 15 (4 female) volunteers (mean age: 26.3 ± 7.5 years) drawn from the staff and student body at the University of Birmingham. All self-reported being right-handed, and this was confirmed with the Edinburgh Handedness Inventory (EHI)

(Oldfield, 1971); mean score = 98.7 ± 4.99. All participants were unimpaired and were naïve to the purpose of the study. The study was approved by the University of Birmingham's Science, Technology, Engineering and Mathematics Ethical Review Committee (ERN_15–1573). Participants provided informed consent in writing prior to taking part.

2.2. Apparatus

The experiment was conducted in the Motor Cognition Laboratory within the School of Sport, Exercise and Rehabilitation Sciences at the University of Birmingham. The room was kept silent to help participants' concentration, and the workspace was free from any unnecessary objects.

Limb movements were recorded by a 3-camera motion capture system (ProReflex, Qualisys Ltd., Sweden) sampling at a rate of 200 Hz. Small, reflective spherical markers tracked by the cameras were placed on the index fingernail of each hand using double-sided sticky tape.

A mirror (50 cm × 40 cm) was placed (short side down) on the table, its edge flush with the table edge and aligned to the participant's mid-sagittal plane (see Fig. 1). The mirror was held in place by two small bespoke wooden mounts. The participant's hands initially rested on the table at either side of the mirror and at an equal distance from it. A template, printed on an A0 piece of paper and fixed to the table. At either side of the mirror and an equal distance from it, an 8.5 cm diameter circle was printed and formed a visual template to guide the participants' circle-drawing movements. The distance between the circle centres was 35.8 cm. A small cross at

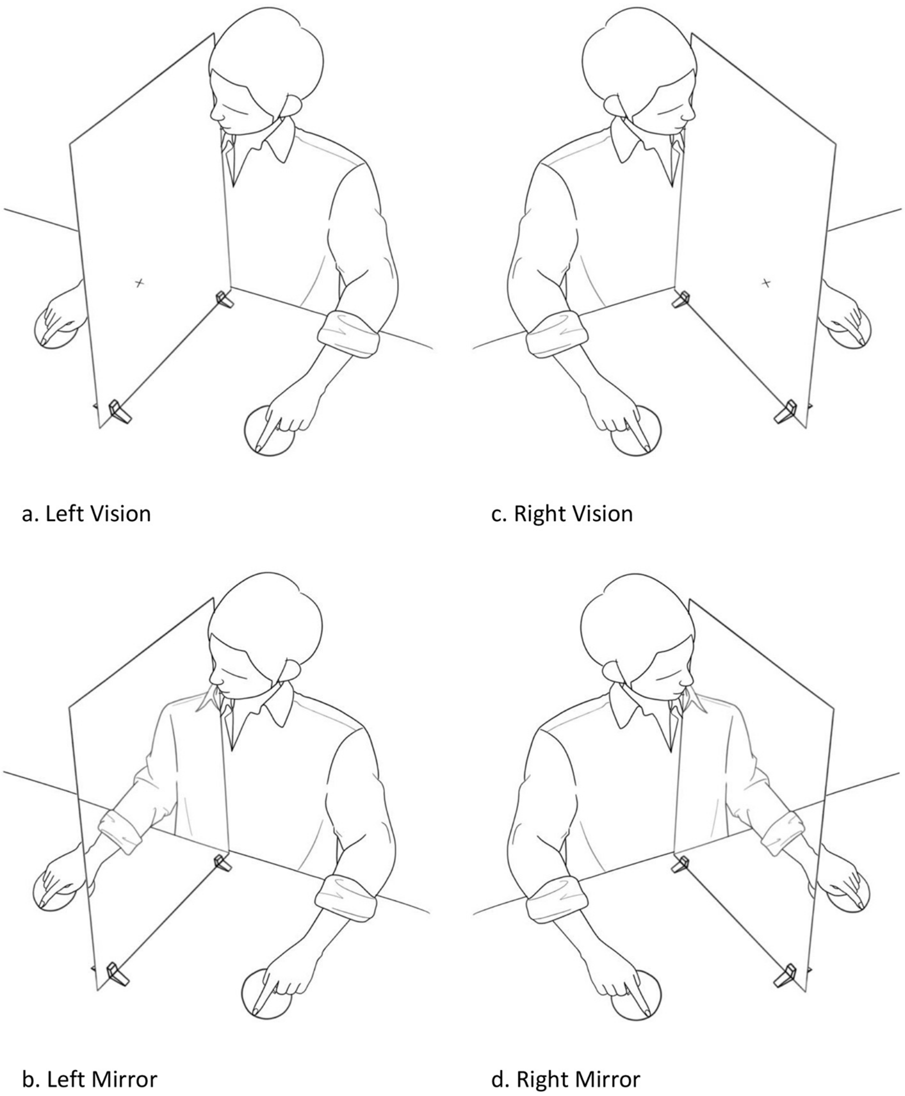

Fig. 1. Experimental conditions. Four conditions were made by crossing the Head side (Left, Right) and Mirror (Mirror, Vision) variables. The Head side presents where the head is placed relative to the mirror, and the Mirror shows whether facing the mirror or the opaque screen. When the mirror was present, participants looked at the tip of the index finger in the mirror. When the mirror was removed, the vision was fixed at the 'x' mark.

the *top* ('12 o'clock') of each circle (30 cm from the table edge) indicated the starting position for the participant's index fingertips on all trials.

2.3. Task, design and procedure

Trials required participants to draw continuous self-paced circles with both hands for 15 s. Although the pace of circle drawing was not formally constrained, participants were asked to move at an approximate rate of one circle per second. Circles were drawn with pointing index fingers, keeping the fingertips in contact with the template surface at all times. Upper limb movements were largely restricted to involving motion at the shoulder and elbow joints, but wrist and finger movements were not physically restricted. The index fingertips were the only points of contact between the participant and the table. Starting at the starting position on the templates, movements proceeded in a synchronised mirror-symmetrical manner, with the right hand moving in a clockwise (CW) direction and the left hand in a counterclockwise (CCW) direction. Given the trial length (15 s) and movement speed, participants completed approximately 15 circles with each hand on every trial.

Participants performed 40 trials during Experiment 1, and there were four conditions; participants completed ten trials per condition. The four conditions (see Fig. 1) were as follows; left hand visible without mirror (Left Vision), left hand visible with mirror (Left Mirror), right hand visible without mirror (Right Vision) and right hand visible with mirror (Right Mirror). The 'Left, Right' in the condition represents which side of the mirror the head was positioned and this was defined as 'Head side'. Conditions were randomised across trials. For *Mirror* conditions, the reflective surface of the mirror was on the same side as the participant's head and the participant was instructed to direct their vision to the reflection of their hand in the mirror. For *Vision* conditions, the mirror was positioned the opposite way around so that the opaque surface was at the same side as the participant's head. For these trials, the participant was instructed to direct their vision only towards a fixation cross that was placed on the opaque surface of the mirror spatially consistent with the position of the reflected hand in the *Mirror* conditions. Participants were observed throughout the experiment to ensure they followed instructions.

Prior to the experiment, participants completed the EHI and were given written instructions about the procedure to read. Any subsequent questions were answered. Participants then proceeded to complete a small number of practice trials before the experimental trials began. Where necessary, a metronome was used during practice trials to indicate the approximate speed of movements. Trials began with a verbal 'go' signal from the researcher and ended with a verbal 'stop' signal. A short rest was given between trials, and 5 min of a scheduled break was given after 20 trials.

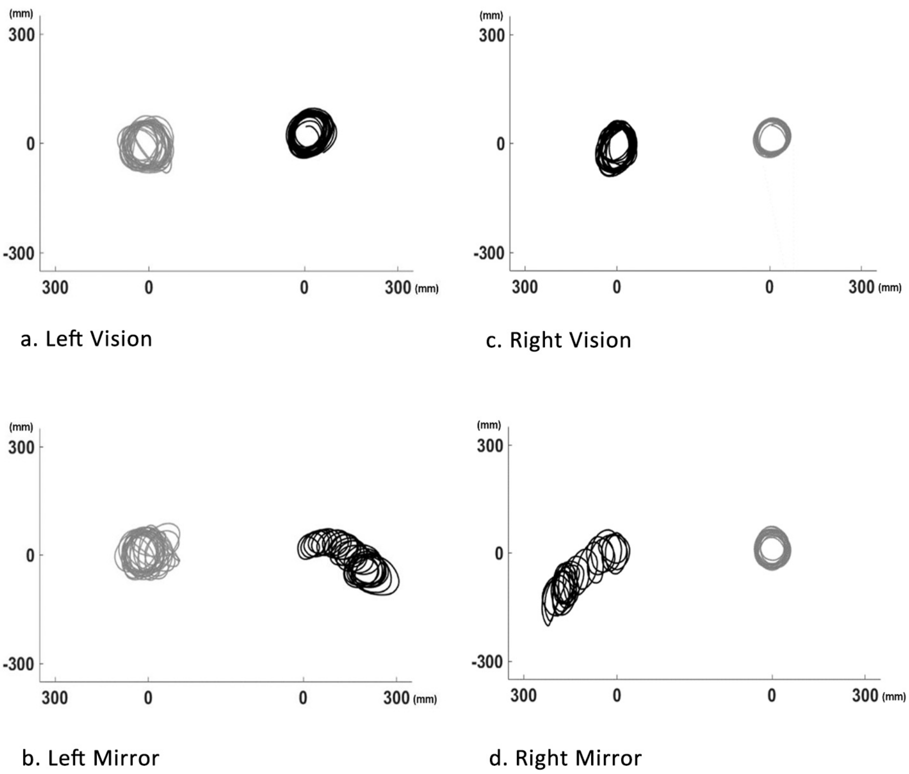

Fig. 2. Hand trajectories of a representative trial for each condition. The grey lines represent the seen hands' trajectories, and the black lines represent the unseen hands' trajectories. The positional drift of the unseen hand appears in Mirror conditions, and it gradually increases.

2.4. Data analysis

Kinematic data were exported and analysed offline using bespoke software (Matlab 2019b, Mathworks Inc., Natick, MA, USA). Signals were rectified and filtered with a 4th-order low-pass Butterworth filter using a cut-off of 20 Hz (see Fig. 2). The main variables of interest were positional drift, circle circumference, and inter-limb asynchrony. The analysis proceeded by separating the continuous circles into individual circles. The first cycle of each circle started from the minimum value for the x-axis in the left hand (i.e. the furthest point leftwards) and the maximum value for the x-axis in the right hand (i.e. the furthest point rightwards). The same subsequent points for each circle represented the end of the completed circle and the start of the new circle. Dependent variables were defined accordingly:

Positional drift - calculated for each trial and represented by a straight line between the centre of the circle farthest from the centre of the first drawn circle. The centre of the circle was determined by taking the values halfway between the maximum and minimum values in the x and y-axis.

Circumference – the trajectory length of each circle. Since a circle is drawn by combining the coordinates that comprise a cycle, the circumference length was estimated by sequentially adding the distance between the coordinates from the starting point to the final point of each cycle. The distance between the two coordinates was calculated using the Pythagorean theorem. The formula is as follows: $d = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$.

Inter-limb asynchrony - calculated at the end of every individual circle by comparing the frame number at which each limb reached this point. In each cycle, the frame number of the right limb was subtracted from that of the left limb. Thus, a negative value referred to a left limb lead (right limb lag) and positive values referred to a right limb lead (left limb lag) (Punt et al., 2013). Since movement was captured at 200 frames/s, a difference of one frame represents 5 msec (0.005 s).

2.5. Statistical analysis

Data were analysed by using SPSS (IBM SPSS Statistics, Version 25.0. Armonk, NY, USA). They were checked to ensure they met normality assumptions for parametric analyses. Individual mean values were calculated for the factors of interest. *Positional drift* and

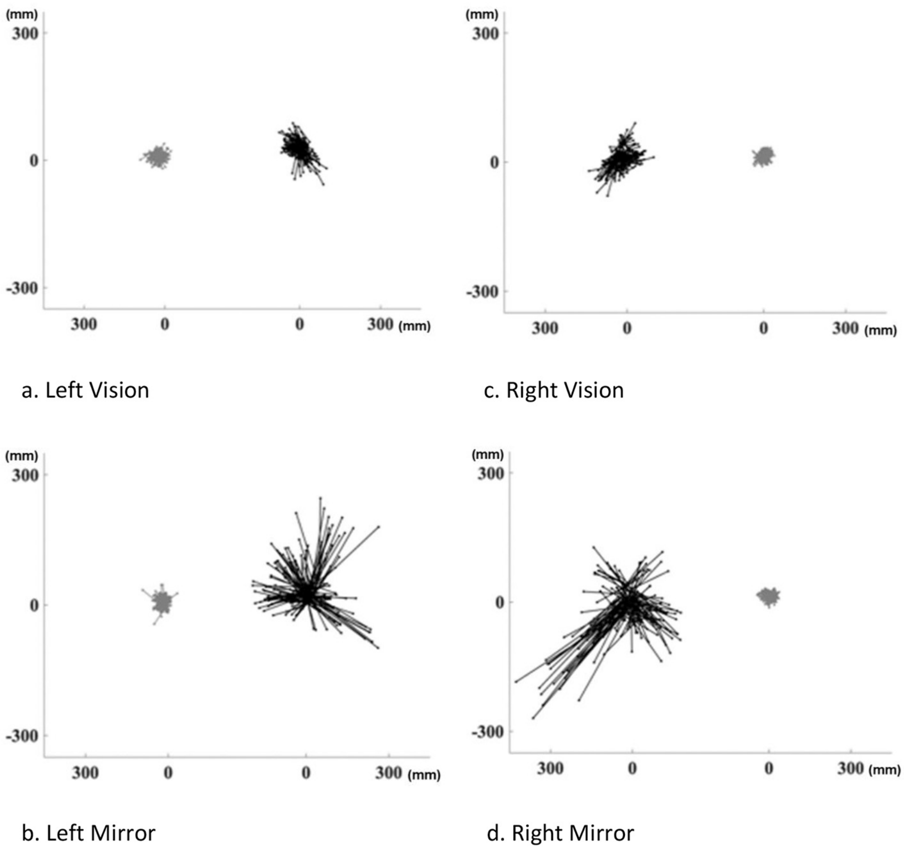

Fig. 3. Positional drift in Experiment 1. Lines represent positional drift on every trial as a function of the Head side, Mirror and Hand. The ends of each line reflect the centre of the first circle to the centre of the furthest circle drawn. The grey lines represent the seen hands' positional drift, and the black lines represent the unseen hands' positional drift.

Circumference data were analysed via a 2 × 2 × 2 (*Head side* [left, right] × *Mirror* [mirror, vision] × *Hand* [seen, unseen]) analysis of variance (ANOVA) with repeated measures. *Inter-limb asynchrony* data were analysed via a 2 × 2 (*Head side* [left, right] x *Mirror* [mirror, vision]) ANOVA with repeated measures. The threshold for statistical significance was set to $p < 0.05$.

Where there were interactions, simple effects reported were corrected for multiple comparisons (Bonferroni).

3. Experiment 1 results

3.1. Positional drift

Fig. 3 shows drift lines that represent the extent of positional drift for every trial; for both hands and for each condition. Fig. 4 shows the related group mean values. There were significant main effects of *Mirror*, $F(1,14) = 72.86$, $p < 0.001$, $\eta_p^2 = 0.839$ and *Hand*, $F(1,14) = 174.21$, $p < 0.001$, $\eta_p^2 = 0.926$ and also a *Mirror* x *Hand* interaction, $F(1,14) = 88.92$, $p < 0.001$, $\eta_p^2 = 0.864$. As can be seen in Fig. 4, the interaction is explained by the impact of the *mirror* on the *unseen* hand. Accordingly, the positional drift of the *seen* hand was comparable regardless of whether the mirror was in place or not, $F(1,14) = 0.01$, $p = 0.926$, $\eta_p^2 = 0.001$. However, the positional drift of the *unseen* hand was significantly greater when the mirror was in place, $F(1,14) = 82.13$, $p < 0.001$, $\eta_p^2 = 0.854$.

3.2. Circumference

Across the experiment, mean circumference was larger when the mirror was in place (mean = 266.15 ± 38.71 mm) than when replaced by an opaque screen (mean = 255.75 ± 45.34 mm), leading to a significant main effect of *Mirror*, $F(1,14) = 5.03$, $p = 0.042$, $\eta_p^2 = 0.264$. Additionally, the *seen* hand (mean = 267.35 ± 39.57 mm) made circular movements that had a significantly larger circumference than the *unseen* hand (mean = 254.55 ± 44.28 mm), $F(1,14) = 13.90$, $p = 0.002$, $\eta_p^2 = 0.498$. However, *Head Side* x *Hand*, $F(1,14) = 8.69$, $p = 0.011$, $\eta_p^2 = 0.383$, *Mirror* x *Hand*, $F(1,14) = 13.85$, $p = 0.002$, $\eta_p^2 = 0.497$ and *Head Side* x *Mirror* x *Hand*, $F(1,14) = 8.68$, $p = 0.011$, $\eta_p^2 = 0.383$ interactions suggested a more complex relationship between factors. The results of the complex interaction are shown in Fig. 5. When the head was to the *left*, there was no *Mirror* x *Hand* interaction, $F(1,14) = 0.96$, $p = 0.344$, $\eta_p^2 = 0.064$, with the *seen* (left) hand consistently drawing larger circles. However, when the head was placed to the *right*, there was a *Mirror* x *Hand* interaction, $F(1,14) = 22.66$, $p < 0.001$, $\eta_p^2 = 0.618$. Here, the *seen* (right) hand only drew smaller circles in the *no mirror* condition, $F(1,14) = 7.70$, $p = 0.015$, $\eta_p^2 = 0.355$. In the mirror condition, circumferences were comparable, $F(1,14) = 0.10$, $p = 0.753$, $\eta_p^2 = 0.007$.

3.3. Inter-limb asynchrony

Across the experiment, there was a small right (dominant) hand lead (mean = 39.38 ± 47.38 ms). When the head was positioned to the left (i.e. looking in a rightwards direction), the right-hand lead was increased (mean = 59.59 ± 47.30 ms). The right-hand lead was reduced when the head was positioned to the right (i.e. looking in a leftwards direction) (mean = 19.17 ± 38.55 ms). There was a related significant main effect of *Head Side*, $F(1,14) = 22.83$, $p < 0.001$, $\eta_p^2 = 0.620$. However, as can be seen in Fig. 6, these differences

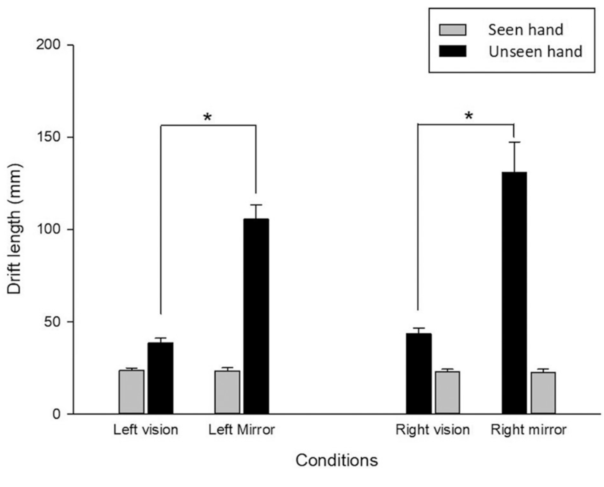

Fig. 4. Mean drifts for the four conditions in Experiment 1. Error bars denote standard error, and asterisks denote statistical significance. Seen hand and unseen hand depend on the Head side. In the case of the left head side, the seen hand becomes the left hand, and the unseen hand becomes the right hand. In the case of the right head side, the seen hand is changed to the right hand and the unseen hand to the left hand.

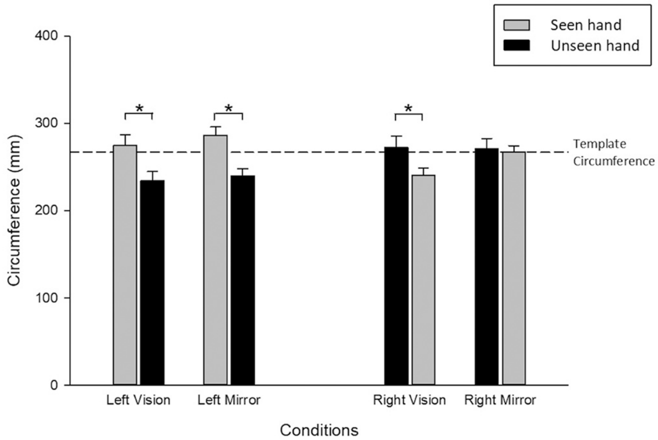

Fig. 5. Mean circumferences for the four conditions in Experiment 1. Error bars denote standard error, and asterisks denote statistical significance. Seen hand and unseen hand depend on the Head side. In the case of the left head side, the seen hand becomes the left hand, and the unseen hand becomes the right hand. In the case of the right head side, the seen hand is changed to the right hand and the unseen hand to the left hand.

were modulated further by the presence of the mirror. Indeed, the presence of the mirror (and subsequent vision of an illusory hand) appeared to accentuate the changes in asynchrony as a result of *Head Side*. There was a resulting *Head Side* x *Mirror* interaction, $F(1,14) = 6.80$, $p = 0.021$, $\eta_p^2 = 0.327$. However, exploring the simple effects of this interaction only revealed a *Mirror* effect when the head was positioned to the left, $F(1,14) = 7.05$, $p = 0.019$, $\eta_p^2 = 0.335$. The corresponding effect when the head was positioned to the right was not statistically reliable, $F(1,14) = 3.98$, $p = 0.066$, $\eta_p^2 = 0.221$.

An independent *t*-test was also performed to compare each condition's interlimb asynchrony to zero (representing perfect interlimb synchrony). Aside from the *Right Mirror* condition, $t(14) = 1.13$, $p = 0.277$, interlimb asynchrony was significantly different in all other conditions, *Left Vision*, $t(14) = 5.39$, $p < 0.001$, *Left Mirror*, $t(14) = 5.16$, $p < 0.001$, *Right Vision*, $t(14) = 2.69$, $p = 0.018$.

4. Experiment 1 discussion

In this experiment, we examined the kinematics of bimanual circle-drawing movements in unimpaired participants with and without mirror visual feedback. Participants completed a series of 15-s trials (drawing approx. One circle per second) under four different conditions. Circle circumference and inter-limb asynchrony were both significantly modulated by the mirror and showed some similarities with findings from previous studies. These findings will be discussed in more detail in the *General Discussion* (see later). However, the most striking feature of the experiment was the very marked positional drift of the unseen hand during mirror

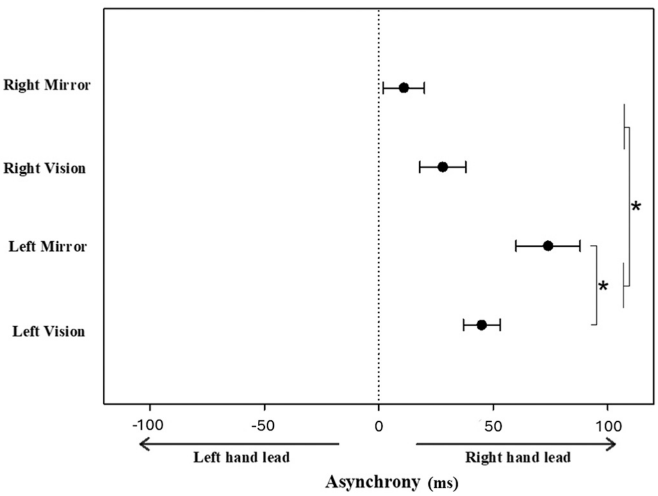

Fig. 6. Mean inter-limb asynchronies for the four conditions in Experiment 1. Error bars denote standard error, and asterisks denote statistical significance. Seen hand and unseen hand depend on the Head side. In the case of the left head side, the seen hand becomes the left hand, and the unseen hand becomes the right hand. In the case of the right head side, the seen hand is changed to the right hand and the unseen hand to the left hand.

visual feedback conditions. While some drift of the unseen hand was also observed during no mirror conditions (i.e. when the vision of the limb was simply occluded), the marked increase in the drift when the mirror was present was remarkable (see Fig. 2). Indeed, at the end of such trials, participants appeared very surprised by the new position of the limb behind the mirror. At times during the experiment, participants reacted at the end of *mirror* trials with comments such as "I feel stupid", "That's weird", and "This cannot be" in response to finding their unseen hand in a position some distance from where they had expected it to be.

Such feedback relating to the positional drift may have been expected to affect behaviour on subsequent trials. However, the consistency of positional drift observed suggests that receiving this information did not obviously affect subsequent performance. There could be a number of reasons for this. For example, as was indicated in the method section, condition was randomised across trials; i.e., two identical mirror trials were never performed consecutively. The persistence of the positional drift may also indicate the strength of the illusion.

The positional drift observed for the unseen hand displayed some consistency with previous studies showing positional errors on reaching tasks but extends these findings to highlight the effects and implications of mirror visual feedback for a continuous task. For instance, under similar mirror conditions, Holmes and colleagues reported how observation of a static hand positioned so there is a small offset between the perceived visual and proprioceptive (felt) positions of the unseen hand, is sufficient to elicit a reaching error (Holmes et al., 2004). However, note this was not the case when the seen and felt positions of the unseen hand were congruent. Subsequent work demonstrated how these errors were enhanced if preceded by a few seconds of active movement (Holmes & Spence, 2005).

In the present study, the starting position was designed so that the perceived seen and felt positions of the unseen hand were congruent. Nevertheless, the unseen hand showed a strong tendency for its position to drift without apparent awareness, often ending a trial a substantial distance away from where it had begun (see Fig. 7). It appears that small corrective movements of the unseen hand in response to small deviations away from the template with the seen hand were sufficient to elicit substantial positional drift across the length of a trial. The continuous task appeared to provide the conditions for these small *corrective* movements of the unseen hand to

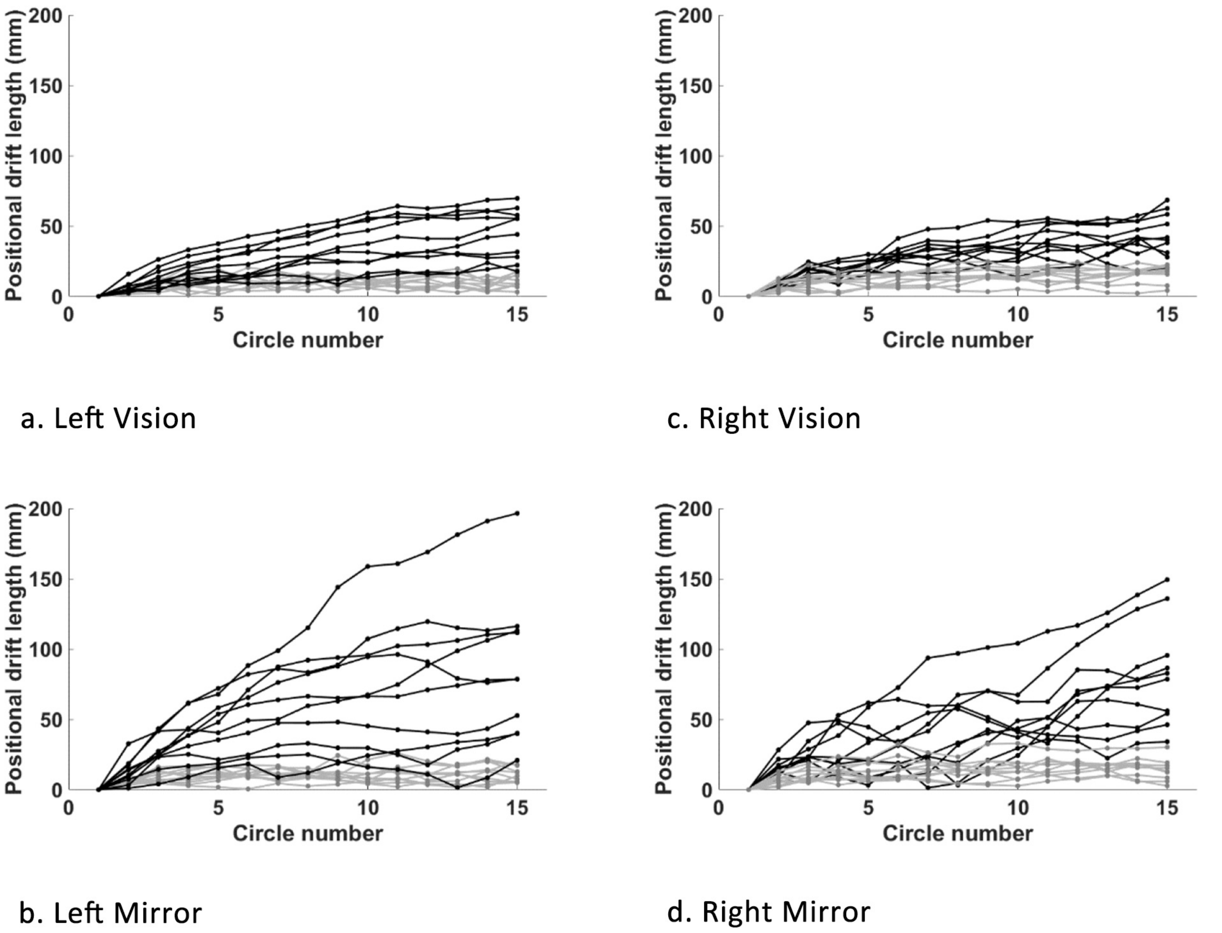

Fig. 7. Development of positional drift within the trials (Experiment 1). This figure shows the development of positional drift that occurred in every trial of each condition from a representative participant who participated in Experiment 1. The grey lines represent the seen hands' positional drift, and the black lines represent the unseen hands' positional drift. This demonstrates how the unseen hand drifts gradually in the Mirror conditions.

contribute incrementally to the considerable positional drift observed in some trials. Indeed, it seems likely that the relatively slow development of positional drift across successively drawn circles was the reason why such large discrepancies between the seen and felt positions of the unseen hand remained unchecked.

The length of trials in Experiment One may also have been a contributing factor, allowing time for the drift to take place (Paillard & Brouchon, 1968). The 15 s selected for trials was considerably longer than those reported by Franz and Packman (2004) and Metral et al. (2014), with neither of these previous studies reporting positional drift. However, perhaps an even more pertinent difference from these previous studies that could account for the considerable drift we observed was our use of a visual template. By providing such clear and unambiguous guidance for movements, participants effectively attempt to *trace* their fingers around the template circles. In doing so, if the seen hand deviated away from the template (even fractionally), providing the mirror illusion was operating, the participant would make small corrective movements of their unseen hand in an attempt to correct hand position in line with the visual information they received. We suggest that this is the mechanism that accounts for the substantial positional drift observed. In a task where visual and proprioceptive feedback contribute to control, it seems likely that providing such explicit visual guidance enhances attention towards visual signals with less attention paid to proprioceptive signals. In Experiment Two, we sought to test this hypothesis empirically by replicating the study in the absence of a visual template.

5. Experiment 2 methods

Fifteen right-handed (EHI mean score = 96.7 ± 8.69) participants (who had not participated in Exp. 1) took part in Experiment 2. They included five males and ten females (mean age: 21.6 ± 3.77) and were students at the University of Birmingham.

The procedure for Exp. 2 was identical to that of Experiment 1, except for the template set-up. In this experiment, the template was removed. Therefore, at the start of each trial, the finger position was guided by the investigator so that the participant could start at the same position as the first experiment. Although the template was removed during the trial, participants spent a few minutes practising over the template (used for Exp. 1) to familiarise themselves with the approximate circle size required and the required hand position.

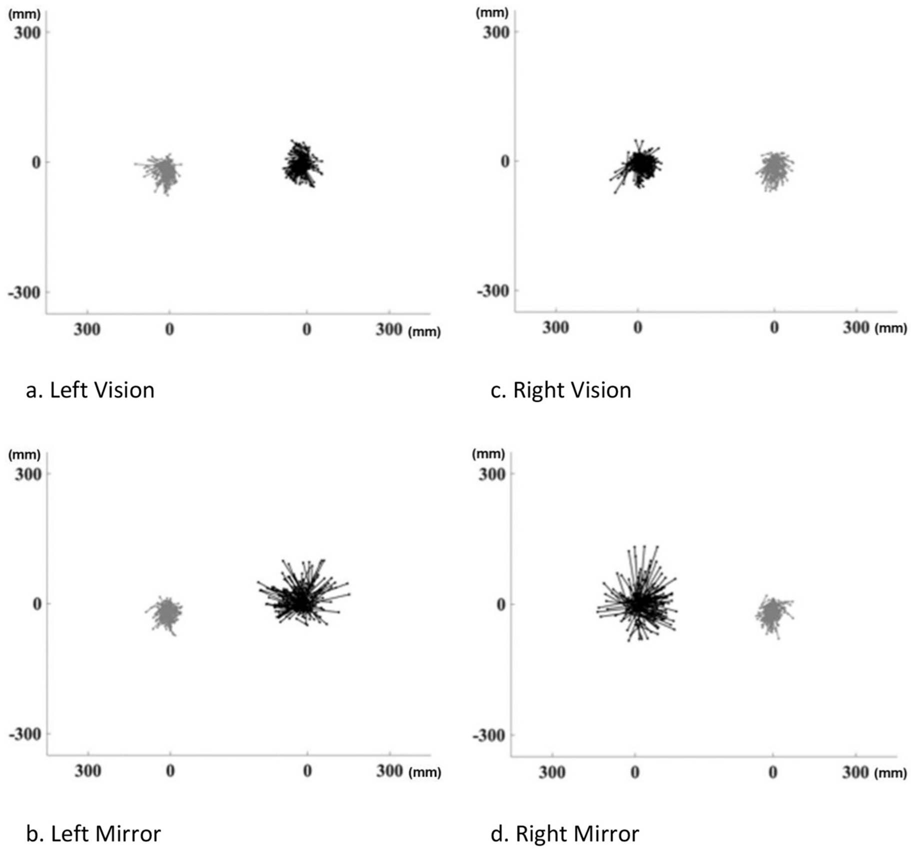

Fig. 8. Positional drift in Experiment 2. Lines represent positional drift on every trial as a function of the Head side, Mirror and Hand. The ends of each line reflect the centre of the first circle to the centre of the furthest circle drawn. The grey lines represent the seen hands' positional drift, and the black lines represent the unseen hands' positional drift.

6. Experiment 2 results

6.1. Positional drift

Fig. 8 shows the extent of positional drift in each hand for every trial from each condition. There were significant main effects of *Mirror*, $F(1,14) = 57.57$, $p < 0.001$, $\eta_p^2 = 0.804$ and *Hand*, $F(1,14) = 82.68$, $p < 0.001$, $\eta_p^2 = 0.855$ and also a *Mirror* x *Hand* interaction, $F(1,14) = 52.35$, $p < 0.001$, $\eta_p^2 = 0.789$. As can be seen in Fig. 9, the interaction is explained by the impact of the *mirror* on the *unseen* hand. Accordingly, the positional drift of the *seen* hand was comparable regardless of whether the mirror was in place or not, $F(1,14) = 0.29$, $p = 0.596$, $\eta_p^2 = 0.021$. However, the positional drift of the *unseen* hand was significantly greater when the mirror was in place, $F(1,14) = 67.48$, $p < 0.001$, $\eta_p^2 = 0.828$.

6.2. Circumference

The ANOVA revealed a significant main effect of *Mirror*, $F(1,14) = 26.06$, $p < 0.001$, $\eta_p^2 = 0.651$; circumferences were larger when the mirror was in place (mean = 323.50 ± 47.25 mm) than when replaced by an opaque screen (mean = 307.97 ± 41.48 mm). There were no other significant main effects or interactions (see Fig. 10).

6.3. Inter-limb asynchrony

As with Experiment 1, there was a small right (dominant) hand lead across this experiment (mean = 16.91 ± 36.81 ms). Similarly, when the head was positioned to the left (i.e. looking in a rightwards direction), the right-hand lead was increased (mean = 38.96 ± 31.68 ms). This right-hand lead became a small left-hand lead when the head was positioned to the right (i.e. looking in a leftwards direction) (mean = −5.15 ± 27.33 ms). There was a related significant main effect of *Head Side*, $F(1,14) = 35.41$, $p < 0.001$, $\eta_p^2 = 0.717$. However, as can be seen in Fig. 11, these differences were again modulated by the presence of the mirror. The presence of the mirror (and subsequent vision of an illusory hand) accentuated the changes in asynchrony as a result of *Head Side*. Accordingly, there was a *Head Side* x *Mirror* interaction, $F(1,14) = 22.75$, $p < 0.001$, $\eta_p^2 = 0.619$. Exploring the simple effects of this interaction revealed a *Mirror* effect both when the head was positioned to the left, $F(1,14) = 17.03$, $p = 0.001$, $\eta_p^2 = 0.549$, and when the head was positioned to the right, $F(1,14) = 10.97$, $p = 0.005$, $\eta_p^2 = 0.439$.

An independent *t*-test was also performed to compare each condition's interlimb asynchrony to zero (representing perfect interlimb synchrony). There was considerable interlimb asynchrony in the left sided conditions, *Left Vision*, $t(14) = 3.25$, $p = 0.006$, *Left Mirror*, $t(14) = 7.29$, $p < 0.001$, but not in the right sided conditions, *Right Vision*, $t(14) = 0.84$, $p = 0.417$, *Right Mirror*, $t(14) = -2.04$, $p = 0.061$.

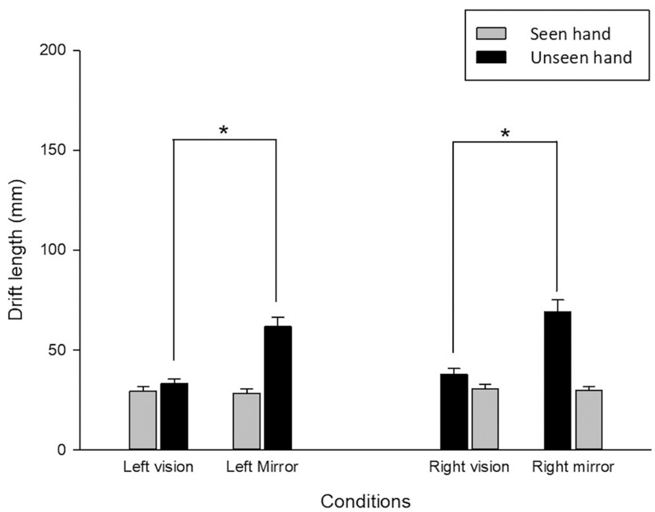

Fig. 9. Mean drifts for the four conditions in Experiment 2. Error bars denote standard error, and asterisks denote statistical significance. Seen hand and unseen hand depend on the Head side. In the case of the left head side, the seen hand becomes the left hand, and the unseen hand becomes the right hand. In the case of the right head side, the seen hand is changed to the right hand and the unseen hand to the left hand.

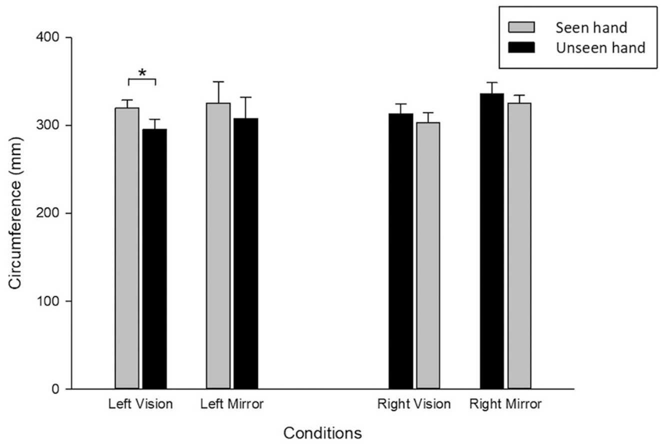

Fig. 10. Mean circumferences for the four conditions in Experiment 2. Error bars denote standard error, and asterisks denote statistical significance. Seen hand and unseen hand depend on the Head side. In the case of the left head side, the seen hand becomes the left hand, and the unseen hand becomes the right hand. In the case of the right head side, the seen hand is changed to the right hand and the unseen hand to the left hand.

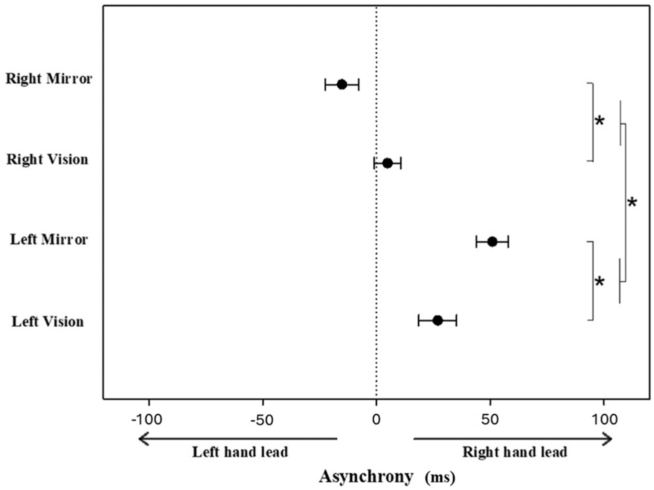

Fig. 11. Mean inter-limb asynchronies for the four conditions in Experiment 2. Error bars denote standard error, and asterisks denote statistical significance. Seen hand and unseen hand depend on the Head side. In the case of the left head side, the seen hand becomes the left hand, and the unseen hand becomes the right hand. In the case of the right head side, the seen hand is changed to the right hand and the unseen hand to the left hand.

7. Experiment 2 discussion

In Experiment 1, it was contended that the marked positional drift observed for the unseen hand during mirror visual feedback trials was enhanced by the presence of a visual template. To investigate this account further, the visual template was removed in Experiment 2. Otherwise, the experiment was a direct replication of Experiment 1. Data from Experiment 2 support the above contention; positional drift was markedly reduced in the absence of a visual template (less than half that observed in Experiment 1). Nevertheless, the positional drift of the unseen hand was still evident and was enhanced in the mirror visual feedback condition (see Fig. 12). Removing explicit visual guidance (i.e. the visual template) did not therefore abolish the positional drift observed in Experiment 1, and we suspect that the visual information that remained available provides the basis for this. In the absence of a visual template, other visual information in the workspace offers a spatial reference for movement. For example, the edge of the table and the borders of the mirror, particularly the lower border as it meets the table, will have provided visual cues. Additionally, although the work surface was designed to be as clear and as clean as possible, small blemishes may have been present or emerged during the course of the experiment and provided further visual information. Such information provides illusory vision of the unseen hand with visuo-spatial reference points leading to related corrective adjustments. These were far less marked in the absence of a visual template but appear to have remained influential. It is unclear whether the relative weighting of illusory vision and proprioception in controlling the position of the unseen hand was different across the two experiments. However, it is likely that more explicit and exacting visual

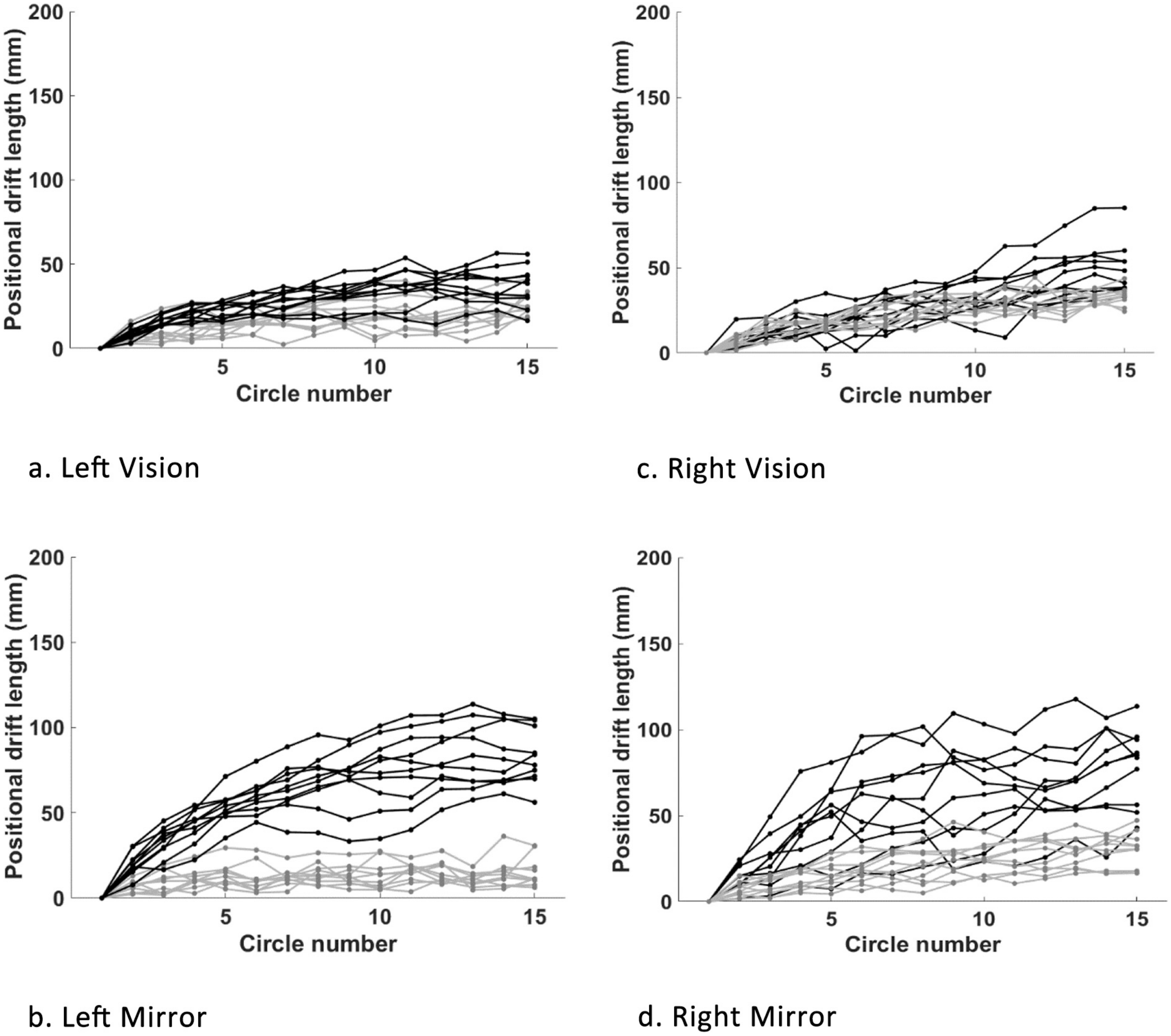

Fig. 12. Development of positional drift within the trials (Experiment 2). This figure shows the development of positional drift that occurred in every trial of each condition from a representative participant who participated in Experiment 2. The grey lines represent the seen hands' positional drift, and the black lines represent the unseen hands' positional drift.

guidance (i.e. by using a visual template as in Experiment 1) enhances the relative contribution of vision.

8. General discussion

8.1. Overview

The experiments reported here both examined the kinematics of bimanual circle drawing movements executed with either a mirror or opaque screen placed in participants' mid-sagittal plane. Where this was a mirror, the setup was comparable with that used for mirror therapy in patient groups (e.g., hemiparetic stroke). As already noted, the marked positional drift of the unseen hand was a feature of both experiments, but different conditions also modulated spatial and temporal coupling. These findings are discussed in turn below before considering the wider implications of the work for theory and practice.

8.2. Positional drift

Although participants behaved as instructed by making reliable circular movements with both hands that were largely synchronised, the position of the unseen hand showed a very strong tendency to drift away from its starting position when the mirror was in place. This occurred whether the unseen hand was the dominant (right) hand or the non-dominant (left) hand.

While the analysis conducted captured the maximum distance that the limbs moved away from the starting position within a trial, it is important to recognise that observation during trials suggested this was not due to large deviations for any single movement. Rather, the overall large deviations appeared to be caused by small but repeated (and consistent) deviations away from the starting position on consecutive movements. These small deviations appeared to cumulate, resulting in the overall large deviations observed (see Figs. 7 and 12).

The substantial positional drift of the unseen hand was a feature for the mirror condition of both experiments but was far more pronounced in Experiment 1 when there was a visual template guiding movement. Indeed, positional drift observed in the unseen hand was almost double when a visual template was present. Perhaps the most satisfactory explanation for this lies in the impact of specific visual information on the recognition of 'error'. In the presence of a visual template guiding the circle-drawing movements, any deviation of the index finger away from this (however small) may be perceived as an error for the illusory limb. Providing the illusion is intact, participants then modify movements of their unseen limb in order to correct for the perceived error. This of course, has no impact on the perceived error as this is generated by the seen limb. As movements of the seen limb are relatively consistent, the perceived error remains and subsequent corrective movements of the unseen limb continue, resulting in the large positional drift reported. While the same process appears to be the case in the absence of a visual template (Experiment 2), the perceived errors may appear less explicit and corrective movements of the unseen hand subsequently less pronounced. It should be noted that the explanation here is speculative. In order to demonstrate this relationship, one would need to monitor deviations by the seen limb on a movement-by-movement basis and then examine whether subsequent movements of the unseen limb were modified to 'correct' for the illusory visual information. The continuous and relatively complex nature of circle-drawing as a task in this study did not allow such an analysis to be easily undertaken here. Nevertheless, such an investigation could be of significant value. In addition to providing a more robust account of the explanation for positional drift observed in the unseen limb, by examining the congruence between the perceived error of the illusory limb and subsequent correction of the unseen limb, such an analysis has the ability to track *how the participants perceive their illusory limb (ownership)*, and *whether participants feel they are the author of the illusory limb (agency)* (Gallagher, 2000; Haggard, 2005) from moment to moment. This would be significant as to date, assessment of ownership and agency over the illusory limb is limited to retrospective and subjective ratings (Moore, 2016).

8.3. Spatial coupling

As highlighted in the introduction to this study, two previous studies examined the impact of mirror visual feedback on bimanual coordination using a circle-drawing task (Franz & Packman, 2004; Metral et al., 2014). Both these studies found the spatial coupling of circles to be enhanced when a mirror was in place. In both experiments reported in this study, there was also evidence of mirror visual feedback eliciting greater spatial coupling between the limbs than when the opaque screen was in place. While together, these studies provide fairly compelling support for the effect, does the enhanced spatial coupling denote anything further? In all cases where mirror visual feedback has led to greater spatial coupling, this has been due to the unseen hand making larger movements than in the other condition tested (e.g., when the mirror was replaced with an opaque screen). Under more simple conditions (i.e., no mirror or opaque screen), Franz (2004) reported that the size of circles was modified by manipulating the focus of attention. When participants paid attention to one particular limb, this limb made larger circular movements. This was true for both non-visual as well as visual attention but was most pronounced for the latter. Our finding that mirror visual feedback also enhanced circle size may in turn, suggest that there was greater attention to the unseen limb in this condition. It has been claimed that mirror therapy enhances attention to the impaired (unseen) limb (Dohle et al., 2009), and the spatial coupling found in the present study seems consistent with this.

8.4. Temporal coupling

When unimpaired participants make continuous bimanual circle drawing movements, it is important to recognise that movements are ostensibly coupled such that the hands reach the top and bottom of each circle drawn at broadly the same time (Kelso et al., 1979). However, it is also known that the very small asynchronies that can be present may be modulated by adjusting conditions (Franz et al., 2002; Swinnen et al., 1996). The two previous studies that examined the impact of mirror visual feedback on bimanual coordination did not find any reliable related modulation (Franz & Packman, 2004; Metral et al., 2014). That was not the case here. In both experiments reported in this study, the presence of mirror visual feedback had a reliable, consistent and intriguing influence on small between-limb asynchronies. Overall, there was a tendency for the dominant (right) limb to lead with a reciprocal non-dominant (left) limb lag. However, when mirror visual feedback was present, this increased the right limb lead when participants experienced a right illusory limb and shifted in the opposite direction (e.g. a reduced right limb lead in Experiment 1 and a left limb lead in Experiment 2) when participants experienced a left illusory limb. This is interesting as these modulations are entirely consistent with what is observed when attention is drawn to the actual limb (Swinnen et al., 1996). In their study, Swinnen et al. (1996) had participants perform bimanual circle-drawing movements while visually monitoring one hand or the other. They too, found a generalised small right-hand lead. Additionally, in their attentional cueing account, they also found that visually monitoring the dominant or non-dominant limb respectively increased or reduced this asynchrony. Consistent with the findings discussed above (temporal coupling), the findings here strongly suggest that mirror visual feedback increases attention to the illusory limb.

9. Conclusion

This study presents two experiments examining the impact of mirror visual feedback on bimanual movements. The findings suggest that a powerful visual illusion *drives* motor control of the unseen limb. Accordingly, the position of the unseen limb was found to drift away from its starting position, with participants seemingly unaware of the relatively large discrepancies between the relative positions of their actual limb and the illusory limb. The positional drift was most apparent when a visual template guided movement. Additional findings reported here relating to spatial and temporal coupling strongly suggest that mirror visual feedback of an illusory limb enhances attention to the unseen limb. This is important as enhanced attention to the impaired limb is a reported mechanism underpinning the effectiveness of mirror therapy for hemiparesis following stroke.

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CRediT authorship contribution statement

J. Kim: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **S.-H. Yeo:** Supervision, Formal analysis, Data curation. **T.D. Punt:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data availability

Due to the sensitive nature of the data, information created during and/or analysed during the current study is available from the corresponding author (Jin Min Kim/j.m.kim@bham.ac.uk) on reasonable request to bona fide researchers.

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