Exp Brain Res (2004) 157: 174–180
DOI 10.1007/s00221-004-1831-3

RESEARCH ARTICLES

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Fooling the brain into thinking it sees both hands moving enhances bimanual spatial coupling

Received: 13 May 2003 / Accepted: 22 December 2003 / Published online: 7 February 2004

Abstract This study examined the hypothesis that the mirror reflection of one hand's movement directly influences motor output of the other (hidden) hand, during performance of bimanual drawing. A mirror was placed between the two hands during bimanual circle drawing, with one hand and its reflection visible and the other hand hidden. Bimanual spatial coupling was enhanced by the mirror reflection, as shown by measures of circle size. Effects of the mirror reflection differed significantly from effects of vision to one hand alone, but did not differ from a control task performed in full vision. There was no evidence of a consistent phase lead of the visible hand, which indicates that the observed effects on spatial coupling were immediate and not based on time-consuming feedback processes. We argue that visual mirror symmetry fools the brain into believing it sees both hands moving rather than one. Consequently, the spatial properties of movement of the two hands become more similar through a process that is virtually automatic.

Keywords Motor processes · Efference copy · Mirror reflections · Spatial coupling · Bimanual symmetry

Introduction

When viewing a mirror placed directly in front of the body along the midline axis that separates the left and right sides, the reflection of one moving hand gives the appearance of symmetrical bimanual movements. The vividness of this illusion was demonstrated elegantly when Ramachandran and colleagues reflected amputees' intact hands producing different grips and postural motions and observed participants' astonishment and surprise at the observable movements of their phantom limbs (Ramachandran and Rogers-Ramachandran 1996; Ramachandran et al. 1996; Ramachandran and Hirstein 1998). An initial interpretation of this observation was that visual information associated with the intact limb's motion, when reflected to give an appearance of the other (amputated) limb, also engages the appropriate sensory areas of the amputated limb. Another possibility (though not mutually exclusive) is that the mirror reflection fools the brain into thinking both hands are in view, and this visual mirror symmetry directly activates central processes associated with movement (even though the limb itself was no longer in existence). The precise parameters of limb movement that are influenced by the mirror manipulation have not been measured.

In a related study, Franz and Ramachandran (1998) investigated whether a form of bimanual spatial coupling would persist even in the absence of feedback processes. We asked normally-intact participants and people with single limb amputation to perform drawing movements on a digitizer tablet under three different experimental conditions. In a single limb control condition, participants were instructed to draw lines with one limb (the intact limb in the case of amputees), and no task was assigned to the other (phantom) limb. In the parallel bimanual condition, participants were instructed to draw lines with one limb (intact limb), and to simulate finger tapping movements of the other (phantom) limb in the same orientation as the line drawing movements. In the orthogonal bimanual condition, participants were instructed to draw lines with one limb (intact) and to simulate twirling movements of the index finger of the other (phantom) limb. For the latter two conditions, instructions were to produce simulated finger movements (rather than whole arm movements) of the phantom because the insertion of finger muscles was below the level of amputation; this would eliminate the possible influence of afferent feedback that might emanate from movements of the residual stump. In all conditions, movement of the limbs was obstructed from view of the participants, and no visual templates were used. Participants were therefore required to guide their movements

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from internal representations (memory). Spatial disruptions in the line drawing tasks were measured and then compared across conditions.

On the basis of findings from normally-intact participants, larger spatial disruption in the orthogonal condition compared to the parallel and single hand control conditions would be interpreted as evidence of spatial coupling between the limbs. Specifically, when attempting to produce circular movements with one limb and linear movements with the other, the lines become circle-like and the circles become line-like. These disruptions in the shapes of trajectories are not observed when both hands are assigned the same shape (Franz et al. 1991; Franz 1997; Franz et al. 1996; see Franz 2003a for review).

Similar to the effects in normally-intact individuals, Franz and Ramachandran (1998) observed spatial coupling when an amputee with the experience of a vivid phantom limb produced the bimanual task in the orthogonal condition. There was significantly more spatial disruption on the line drawing task in the orthogonal condition than in the parallel and control conditions. These results suggest that at least one form of spatial coupling is not dependent on feedback processes from the limb(s). These results also indicate that the neural processes that produce spatial coupling may remain intact even though the physical properties of a limb may be absent. Indeed, related studies have demonstrated that the corpus callosum is one neural structure on which some forms of spatial coupling depend, given bimanual spatial coupling in competitive situations (those involving distinct tasks for the two hands) is substantially reduced in patients with callosotomy (Franz et al. 1996). Moreover, even without a corpus callosum, interference between the hands is minimal in many bimanual cooperative tasks that are unified by a single behavioral goal that was well-learned prior to surgery, although this is not the case with novel bimanual tasks (Franz et al. 2000; see also Franz et al. 2001). As these results imply, clearly there are different levels of spatial coupling influencing bimanual actions (Franz 2003a).

Considering again the above-described studies on amputees, it appears that vivid movement sensation, and consequent bimanual spatial coupling, may occur in amputees who experience a phantom limb, echoing the earlier conclusion that some forms of central (spatial) coupling remain present even after loss of a limb. The primary purpose of the present study was to examine the nature of this form of spatial coupling by closely investigating the effect of the mirror manipulation applied by Ramachandran. Specifically, the aim was to investigate whether the mirror reflection manipulation is powerful enough to influence *motor output properties* in normally-intact participants. We examined this issue by measuring the movement properties in a bimanual circle drawing task while applying the mirror reflection manipulation of Ramachandran.

The task of bimanual circle drawing has been thoroughly investigated in recent years and provides a feasible means of measuring both the spatial and the temporal properties of coupling between the limbs (Carson et al. 1997; Franz 2000a, 2000b, 2003b; Franz et al. 2002; Semjen et al. 1995; Stucchi and Viviani 1993; Swinnen et al. 1996; Wuyts et al. 1996). We hypothesized that specific spatial properties would likely be altered by the use of the mirror reflection, due to the known relation between spatial and visual processes of movement. In bimanual circle drawing, for example, circle size has been shown to alter depending on visual attention to one hand or the other. Specifically, when one limb is attended and the other limb is hidden from view during bimanual circle drawing, circles drawn by the attended limb are produced larger than circles drawn by the unattended limb. These effects are most pronounced when attention is visual, but they also occur when attention is nonvisual (Franz 2003b). Because viewing one's motions in a mirror depends both on vision and on attention processes, the task of bimanual circle drawing seemed suitable to begin this investigation. Moreover, this task involves a common spatial goal for both hands, thereby eliminating the spatial interference that may occur when distinct spatial goals are implemented (Franz et al. 2001; Franz 2003a, 2003b).

The critical question with respect to spatial coupling concerns whether between-hand differences in circle size are altered when the mirror illusion is employed. It was predicted, based on inferences gained from the application of mirror bimanual reflections in amputees, that circle size would be more similar for the tasks of the two hands when the mirror was employed compared to when vision of only one hand was employed.

The task of bimanual circle drawing also provides a means to examine the temporal variable of phase lag between the hands. If the hidden hand consistently lags behind the visible hand, then one cannot rule out the possibility that the performer follows the visual feedback of one hand to guide movement of the other hand. However, if the hidden hand does not consistently lag behind the visible hand, then the effects of the mirror would seem to be somewhat automatic rather than based on time-consuming feedback processes.

Materials and methods

Participants

The participants were 15 undergraduate volunteers, 5 males and 10 females, from the University of Otago. They ranged in age from 18 to 23 years (mean=19.5). They were right handed (mean score=0.78) according to an adapted Edinburgh Handedness Inventory (Oldfield 1971). All procedures herein were approved by the Human Ethics Committee of the University of Otago.

Apparatus

The experiment was conducted in an enclosed soundproof experimental booth. The inner wall of the booth was lined with black curtains to prevent visual distraction or reflection. Participants were seated with the center of the body directly in line with the division between two digitizer tablets (30×30 cm) placed side by side. Magnetic pens that did not leave a visible trace were used to draw. The digitizer tablets were connected to a PC computer and were run by in-house software routines. The *x* and *y* coordinates of each pen's position were recorded at 100 Hz with .0025 cm spatial accuracy.

A wooden box with a mirror attached on one side was placed directly over one tablet so that the mirror would reflect one of the participant's hands while the box hid the other hand from the subject's view (see Fig. 1). The mirror box was 46 cm long, 44 cm wide, and 27 cm high, with a 46 × 38 cm mirror attached on one side. The mirror box had open ends to allow participants to insert their hands. The open ends were covered with a black silk curtain to prevent the participant from seeing one hand or its movement. A cape protruding from the box was placed over the participant's shoulders so that no proximal motion of the arm could be seen (not shown in Fig. 1 so that the apparatus would be clearly visible). The mirror could be exposed to reflect the participant's hand (and its motion), or covered so that no reflection was visible. The mirror box could be positioned to reflect either the left or the right tablet (and hand).

Task, design, and procedure. The experiment involved a within subjects design, with each subject completing four conditions in randomized order. The factors mirror (exposed, hidden) and hand (left, right) were crossed to produce four experimental conditions: vision of left hand with mirror absent (vision left), vision of left hand with mirror present (mirror left), vision of right hand with mirror absent (vision right), and vision of right hand with mirror present (mirror right). In all conditions, one hand and arm was completely hidden from view. Each experimental condition consisted of eight trials, each lasting 8 s. With rest between trials as needed, each testing session lasted approximately 40 min.

On each testing session, the tablets were first calibrated. An instruction sheet was then read aloud to participants and they were given a chance to ask any questions before signing an informed consent form. The experiment then commenced with a demonstration of the task. Participants were given an opportunity to familiarize themselves with the procedures by practicing. They were then instructed to draw at a comfortable pace in a mirror symmetrical manner to produce bimanual circles of constant size through continuous cycles of movement. Participants were instructed to begin each trial with both pens at approximately the 12:00 position on the circles. Note that there was no circle template present, thus subjects drew circles from their own internal representations. Participants were instructed to focus visual attention on the boundary between the tablet and the mirror adjacent to the visible hand's drawing space. The direction of gaze was at about a 45-degree angle with the drawing surface. The same instructions about gaze were given whether the mirror was covered or exposed. This allowed consistency in angle of gaze across conditions, and also ensured that the bimanual illusion was clearly visible from the mirror reflection.

When it was clear that the participant understood the instructions, the first trial began with the experimenter's verbal 'go' command. The tablets began collecting approximately 400 ms after movement commenced, to eliminate any initial variability associated with beginning to draw. After the computer completed data collection for each trial, the experimenter said 'stop'. A short rest was given between trials. After all trials within a condition were collected, the experimenter rearranged the mirror box in preparation for the next condition. After all testing, participants were asked to complete the handedness inventory, and they were then debriefed completely and invited to provide comments.

Data reduction

The first two trials in each condition were regarded as practice, leaving six continuous trials per condition for analysis. The primary variables of interest were circle duration, circle size (radius), and phase difference. Algorithms for the computation of variables have been published in detail in earlier reports (Franz et al. 2002; Franz et al. 2003b), and will be only briefly described here.

Continuous phase was calculated across the trajectories as an initial step, given the trajectories may not form perfect circles, and they may not revolve around a stable center. Tangential angle (TA),

Right mirror

Right vision

Fig. 1 Mirror box apparatus and bimanual drawing setup, showing examples of the right mirror (*left panel*) and right vision (*right panel*) experimental conditions. Not shown are the left mirror and left vision conditions, which were the mirror-image opposite of the conditions shown. The cape worn by subjects is not shown so that the apparatus is clearly visible. In the mirror conditions, participants viewed one side of the mirror, and the reflection of the visible hand created the illusion of bimanual movements (*left panel*) or ‘bearing’ was calculated for each point on the trajectory. A virtual circle of 360 degrees was calculated for each point on the trajectory by searching backward 180 degrees and forward 180 degrees along the TA profile. Instantaneous values of each dependent variable were then computed for each associated point on the circle.

To calculate the radius, the circle center was defined as the midpoint of the x and y values bounded by the virtual circle. The radius was calculated as the distance between the reference point of each virtual circle and the circle center. For the computation of phase difference, an ‘angle of displacement’ was calculated for each hand’s movement, where angle of displacement refers to the orientation of a line drawn from the circle center to a point on the trajectory. The angle of displacement is defined in degrees, using (12:00) as a reference. To compute a measure of phase, the difference between the angles of displacement of the left and right hands was computed. For example, if at some point in time the left hand was at a 30-degree orientation and the right hand was at 15 degrees, the phase difference would be a left hand lead of 15 degrees. For each variable, a measure of variance was also computed to assess consistency in performance.

For mean radius, the signed difference between the hidden hand and the visible hand was computed. The average difference score across trials within each block was entered into a repeated measures ANOVA on the factors visible hand (right, left), × mirror (absent, present) × block (6). Mean phase was analyzed in a similar manner (using phase differences between left and right hand movements). Mean duration was not a difference score, and was therefore analyzed using the within-subjects factors of condition (4) × hand (2) × block (6). Within the text, SE will be used to report standard error of the means.

Results

Given participants were encouraged to draw at a self-selected pace, mean duration was analyzed to give a measure of average cycle period. Mean duration across all participants was 965 ms per circle cycle (SE=66). This drawing speed is within the range observed in past reports of self-paced circle drawing. Importantly, participants drew at similar average speeds in the different experimental conditions, $F_{(3,42)}=1.70$, $p>0.05$, across the two hands, $F_{(1,14)}=2.96$, $p>0.05$, and across blocks, $F<1.00$. Table 1 (first four rows) shows the means and standard errors for the primary dependent variables in each of these four experimental conditions.

The mean circle radius collapsed across all conditions and both hands was 5.7 cm (SE=0.49), also within the range reported in previous studies. There was no hint of a difference in the radius scores depending on which hand was visible, $F_{(1,14)}<1.00$. Of primary importance, difference scores were much larger for mirror absent (difference score=.65 cm) than for mirror present trials (difference score=0.24 cm) on average, $F_{(1,14)}=10.781$, $p<0.002$. In order to illustrate these effects in the context of the actual circle sizes, the mean circle radii and standard errors for each condition are illustrated in Fig. 2 (rather than illustrating difference scores which, of course, do not reveal actual circle size).

As can be seen from Fig. 2, it is clear that with vision to one hand (left vision and right vision conditions) the visible hand drew larger circles than the hidden hand, consistent with previous findings (Franz 2003b). The novel effect is that when the mirror reflection was applied (left mirror and right mirror conditions), this difference in circle size between hands was significantly reduced. The difference between the mirror absent and mirror present conditions was highly significant when the right hand was visible (right vision–right mirror comparison), and marginally significant when the left hand was visible (left vision–left mirror comparison), respectively $F_{(1,14)}=12.39$, $p<0.002$, and $F=4.46$, $p=0.053$. These results support the hypothesis that the mirror reflection enhances bimanual spatial coupling. There were no other interactions on mean radius (all $p>0.05$).

As can be clearly seen from Fig. 2, addition of the mirror reflection appeared to primarily alter radii of the circles drawn by the left hand. This adjustment of the left hand circle size occurred regardless of whether the left

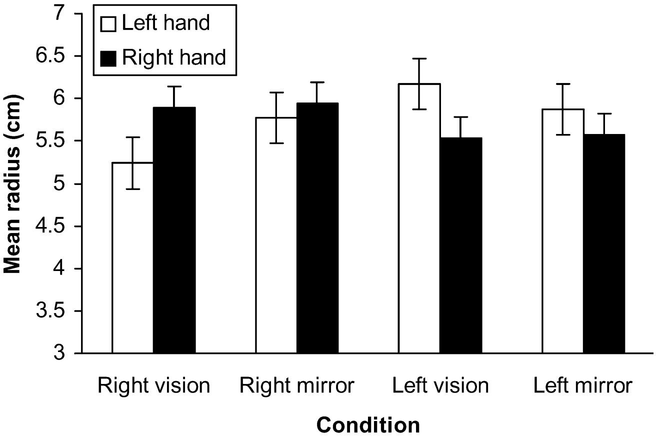

Fig. 2 Mean radius and standard error are shown for the four conditions of the main experiment. In the two conditions with the mirror, the mean radius is more similar for the two hands than in conditions with vision only

Table 1 Means and standard errors of primary dependent variables in the single hand vision, mirror reflection, and full vision control conditions. Variables of mean radius and cycle duration are shown averaged across both hands to illustrate that they are comparable across conditions. Mean phase difference is also shown. Negative values of phase difference indicate a right hand lead

	Mean radius	Cycle duration	Phase difference
Right vision	5.57 cm (.51)	1,000 ms (84)	−3.07 ms (3.2)
Right mirror	5.86 cm (.41)	985 ms (60)	−3.20 ms (4.1)
Left vision	5.85 cm (.53)	932 ms (68)	−1.29 ms (3.2)
Left mirror	5.72 cm (.49)	946 ms (64)	−3.09 ms (3.3)
Full vision control	6.69 cm (.30)	1,088 ms (55)	−2.40 ms (3.0)

hand was in view or the right hand was in view. This effect will be revisited below.

To examine whether one hand consistently led the other, phase difference was analyzed. We hypothesized that if the visible hand consistently leads, then we could not rule out the hypothesis that a time-consuming process of overt monitoring may have guided the hidden hand's movement. An alternative possibility is that a more direct and automatic process is responsible for the engagement of spatial properties of the hidden hand when the mirror is applied. This would be rather immediate, and therefore would not be expected to show up as a consistent lead of the visible hand.

Of primary importance, there was a right hand lead on average, in all conditions. The average lead ranged from –1.3 ms to –3.1 ms (the negative sign indicates a right hand lead), and the miniscule differences across conditions were not close to being reliable, all $F<1.00$. Because it was not the visible hand but rather the right hand that consistently led, the present findings support the hypothesis that a direct and rapid coupling occurs between parameters of the two hands as a result of the mirror reflection.

Discussion

This experiment examined the effects of a mirror reflection of one hand's circle drawing movements on the motor output of a bimanual task. The primary purpose was to examine whether the mirror reflection alters the motor output of a hidden hand's movement. The primary effects were clear and unambiguous. The effect of a larger circle size produced by the visible hand compared to the hidden hand was significantly reduced when the mirror reflection was applied. This effect was found whether the left hand or the right hand was the visible hand. No apparent effects occurred in the temporal parameters (duration or phase) as a result of the mirror manipulation.

There are a few possible ways in which the observed enhancement of spatial coupling could occur as a result of the mirror reflection. One account is that the feedback of one hand's movement is used to actively guide movement of the other hand. This active corrective process based on visual feedback is believed to take some time to operate (Keele and Posner 1968; Carlton 1981). By this hypothesis, we would expect the hidden hand to lag behind the visible hand. Our data clearly do not support this account. An alternative account is that a more rapid and direct form of coupling occurs between the visual information and the processes governing motor output of the hidden hand. This may require the operation of feedforward or efference copy that allows for a rapid speed of information transmission between the perception of movement and the motor output (Franz and Ramachandran 1998); or this process could operate on the global properties of the trajectory (i.e., on the internal representation of the circle: i.e., Franz et al. 1991; Franz 2003a, 2003b). Either of these processes would have to allow for rapid, almost automatic, alterations in the movement plan. The results on phase lag clearly support the hypothesis that coupling occurs in a rapid manner rather than as a result of active monitoring of feedback, given that the hidden hand did not consistently lag behind the visible hand.

One might probe further into the nature of the effects of the mirror. Are the effects on spatial coupling the result of application of the mirror per se? Or, does the visual illusion of actually seeing two hands moving increase bimanual spatial coupling between the hands?[1] A possible way to test this issue would be to allow participants to see both hands while performing the bimanual drawing task and then compare the present mirror conditions with the new control condition using full vision. If the full vision condition produces results that are identical to those found in the mirror conditions, then findings would support the hypothesis that enhanced bimanual spatial coupling is due to the illusion that the participant is seeing both hands moving in a symmetrical manner. In contrast, if the full vision condition produces different results from the mirror condition, then findings based on application of the mirror would remain unexplained.

In a control experiment on 15 naïve subjects of approximately the same description as in the main experiment, bimanual circle drawing data were collected under full vision conditions (allowing subjects to see both hands). The methods were identical to those employed earlier, except that full vision of both hands was allowed, no mirror box was used, and only one condition was tested. We then conducted between-subjects comparisons of all dependent variables across mirror and full vision conditions.

It is perhaps important to point out that the comparison between the left mirror condition and the full vision control would not be clearly interpretable, due to issues related to hand dominance. Recall that in the main experiment, the left hand adjusted its circle size to accommodate that of the right hand when the mirror was applied (compared to vision only conditions), regardless of which hand was mirrored (see Fig. 2). In addition, the right hand was the lead hand, on average, in all conditions (see Table 1). These findings illustrate the well-known property that the right hand is dominant in bimanual symmetrical movements, especially for right-handed subjects (Carson et al. 1997; Franz 2000a, 2000b, 2003a, 2003b; Franz et al. 2002; Semjen et al. 1995; Stucchi and Viviani 1993; Swinnen et. al. 1996; Wuyts et al. 1996). There is also strong support for the claim that the right hand tends to be the primary focus of attention during bimanual performance (Franz 2003b; Peters 1981, 1985), perhaps accounting for the hand dominance effects observed in the present study. With the right hand in view, these two properties (hand dominance and attention dominance) both favor the right hand, thereby allowing for direct interpretations of the comparison between the full vision control condition and the right mirror condition. However, this is not the case for the corresponding

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[1] We thank an anonymous reviewer for suggesting we conduct the additional control experiment.

comparisons involving the left mirror condition because the dominant right hand is hidden in one condition (left mirror) and visible in the other (full vision). Our conclusions, therefore, are based only on data from the comparison of right mirror versus full vision conditions.

The results for the full vision versus right mirror conditions were clear and unambiguous. There was absolutely no hint of a difference in the radius scores produced in the two conditions, nor was there any effect on mean phase difference, both $F_{(1,28)}<1.00$. In addition, mean duration was not reliably different across the two conditions, $F_{(1,28)}=1.748$, $p>0.05$. The means and standard errors for each variable in the full vision condition appear with the other conditions in Table 1. These results strongly support the argument that the mirror reflection results in the illusion that both hands are in view, and this visual symmetry of apparent bimanual movement enhances spatial coupling of the two hands in a manner similar to actual vision of both hands.

Our findings are consistent with the hypothesis that visual capture (Rock 1966) of the observed mirror symmetry promotes fusion of the visual symmetry on the proprioception of the moving hands (see Rosetti et al. 1995 for experiments using unimanual reaching). This proposed process of binding the visual information with the proprioception of movement would have to be rather immediate, given there is no evidence that the visible hand consistently led the hidden hand. One possibility is that the corpus callosum, which is critical to some forms of bimanual spatial coupling (Franz et al. 1996), enables the coactivation of both hemispheres when visual symmetry is perceived. Accordingly, this coactivation would ensure that fusion of visual and proprioceptive information occurs rapidly.

Another possibility is that bimodal neurons (also referred to as ‘mirror neurons’: Gallese et al. 1996) provide a direct interface between seen actions and produced actions; although this hypothesis would extend what is currently known about these neurons because the requirement would be that they respond not only to an external agent but also to one’s own reflection in a mirror.

Another hypothesis that is tempting to invoke is derived from studies on tracking of predictable targets.[2] In an elegant set of studies on grip force adjustments using hand-held loads, Flanagan and Wing demonstrated that modulations in grip force occur in parallel with changes in load. This 0 lag in the modulation of grip force is suggestive of a forward model in which the load force on the hand is predicted and incorporated into the internal model (Flanagan and Wing 1993, 1994, 1997). Applying this type of idea to the present study, it is reasonable that the visible hand that is reflected in the mirror acts as a highly predictable target, especially given its movement is governed under the subject’s voluntary control. The hidden hand might actually track this highly-predictable target with virtually a 0 lag, consistent with the findings of Flanagan and Wing. Indeed, this framework would appear to generalize to bilateral effectors, based on a related experiment performed sometime earlier that required subjects to produce grip force adjustments based on frictional properties of an object using one hand followed by grip force adjustments using the other hand on sequential trials. Stored information related to frictional properties of the object that resulted in adjustments in grip force appeared to influence subsequent trials performed by the other hand (Johansson and Westling 1984). This type of bilateral access of the internal model would be necessary to account for the present findings given the circle size of the left hand movements adjusted to that of the right hand (in comparison with vision only conditions), even when the left hand’s predictable target was the visible one. In other words, if the predictable target information directly updated an internal representation that is accessible to both hands, then this hypothesis seems plausible.

In sum, although the precise theoretical explanation and neural mechanisms for the effect remain to be determined, the present findings demonstrate that bimanual spatial coupling is enhanced with the application of a mirror reflection. This enhancement occurs relatively automatically, rather than as a result of more time-consuming feedback-dependent processes.

Acknowledgements Thanks to Barry Dingwall, Jeremy Anderson, and Michael Bowden for their technical expertise and helpful suggestions. This work was funded in part by Otago Research Grant MFU B26 to Liz Franz

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[2] We again thank a reviewer for this helpful insight.

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