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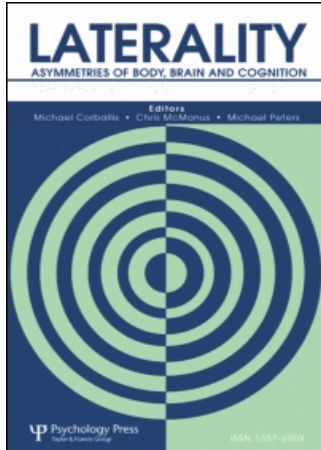
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## Constant error in aiming movements without visual feedback is higher in the preferred hand

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There is convincing evidence for a left hand advantage for the spatial planning of aiming movements in right-handers. However, little is known about equivalent proficiency in left-handers. Therefore, 48 participants (24 right-handers and 24 left-handers) performed aiming movements of the hand without visual feedback. While the variable aiming error tended to be lower for the preferred hand, the constant aiming error was consistently lower for the non-preferred hand. Data are consistent with the idea of a spatial accuracy advantage for the controller of the non-preferred hand. Data from an ambidextrous participant suggest that this functional difference might be innate rather than acquired through practice.

Handedness is usually assessed by asking people which hand they use more often in everyday tasks (e.g., Coren, 1993; Oldfield, 1971). Approximately 90% of the Western adult population report an overall preference for the right hand (e.g., Annett, 2004; Coren, 1993; Gilbert & Wysocki, 1992; cf. McManus, 2002; Salmaso & Longoni, 1985). However, handedness is not only a question of preference but also one of proficiency. For example, there is usually a clear proficiency advantage for the preferred hand in writing. But there is also evidence that right-handers perform several tasks better with the non-preferred hand. For example, left-hand superiority has been demonstrated for the processing of tactile information (Rudel, Denckla, & Hirsch, 1977; Witelson, 1974). Furthermore, unimanual aiming movements are planned faster for the left as compared to the right hand (Barthelemy & Boulinguez, 2001; Mieschke, Elliott, Helsen, Carson, & Coull, 2001; Velay & Benoit-Dubrocard, 1999; Velay, Daffaure, & Benoit-Dubrocard, 2001). Neely, Binsted, and Heath (2005) demonstrated that the left hand responded

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faster than the right hand in a bimanual reaching task. Boulinguez, Velay, and Nougier (2001a) found a left hand advantage for the preparation of movement direction and for online adjustments of movement amplitude. Roy and MacKenzie (1978) asked blindfolded participants to reproduce spatial locations with their arm or thumb. The thumb-positioning task was better performed with the left than with the right hand. Finally, Guiard, Diaz, and Beaubaton (1983) demonstrated that right-handers make smaller constant errors with their left than with their right hand in unimanual aiming movements without visual feedback.

It has been repeatedly suggested that left hand advantages in right-handers are closely connected with right hemisphere superiority in spatial processing (Barthelemy & Boulinguez, 2001, 2002; Boulinguez et al., 2001a; for right hemisphere superiority in visuospatial processing see also Corballis, 2003). Unfortunately, data about manual asymmetries of visuospatial processing in left-handers are sparse and controversial. Velay and Benoit-Dubrocard (1999) and Velay et al. (2001) found no hand-related reaction time (RT) difference in aiming movements. Boulinguez, Velay, and Nougier (2001b) demonstrated shorter latencies for the left hand with a single-step but not with a double-step reaching paradigm. Nevertheless, they concluded that left-handers, just like right-handers, reveal a right hemisphere advantage for the spatial planning of movements.

We conducted the present experiment to find out whether this hypothesised advantage for spatial planning of movements in left-handers is confined to RT asymmetries or whether it also shows up in terms of movement accuracy. As far as we know, asymmetries in the spatial accuracy of left-handers have never been demonstrated until now. If there really is an overall right hemisphere advantage for spatial planning in right- and left-handers, accuracy advantages should not only be found in the left hand of right-handers (cf. Guiard et al., 1983; Roy & MacKenzie, 1978) but also in the left hand of left-handers. Moreover, as the left hand of left-handers is their preferred hand, not only movement planning but also movement execution should be superior as compared to the right hand. Therefore, accuracy asymmetries between the hands should be even more pronounced in left-handers than in right-handers.

## METHOD

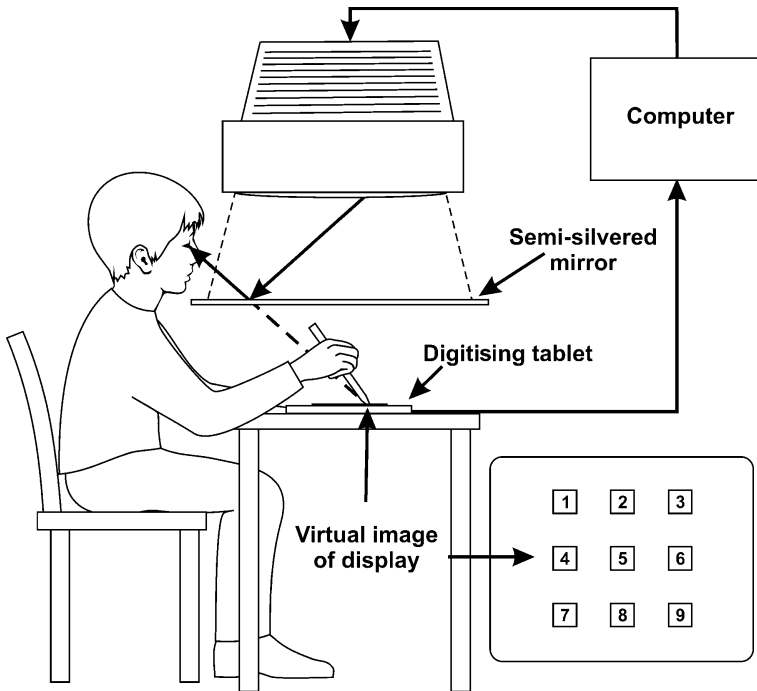
### Participants

The sample consisted of 48 informed volunteers (12 right-handed females, 12 left-handed females, 12 right-handed males, 12 left-handed males), ranging in age from 19 to 42 years ( $M = 22.23$ ,  $SD = 4.23$ ). The participants were recruited from the University of Würzburg and were either paid for their

participation or received course credit. All participants showed maximum hand preference, as determined by the Lateral Preference Inventory (Coren, 1993), except for one left-hander who indicated preference for the left hand in three out of four tasks. Each participant was tested in a single session lasting approximately 15 minutes. The study protocol was performed in accordance with the 2001 Declaration of Helsinki, and verbal consent was obtained from each participant.

## Apparatus and stimuli

Participants sat in front of a digitising tablet (Intuos Graphics Tablet A4) and held a stylus in their hand (see Figure 1). A semi-silvered mirror, which was suspended in a horizontal plane 23 cm above the tablet, prevented direct view of the arm. The position of the stylus as defined by its point was measured on-line and determined successive x and y coordinates of the performed trajectories. The data were sampled at a rate of 50 Hz by a PC



**Figure 1.** Experimental set-up for recording aiming movements of the hand without visual feedback. The position of the hand was measured online via a digitising tablet. A display was projected onto a semi-silvered mirror.

with AMD Athlon Processor (1.01 GHz). A Samsung Sync Master 90092 screen ( $1024 \times 768$  pixels) was fixed to a metal support so that its front was positioned on a horizontal plane 23 cm above the mirror. One pixel measured 0.35 mm on the screen. A display including the aiming targets (Figure 1) was depicted in a mirror-reversed version on this screen. Looking down at the mirror, the participants saw the reflected image of the display. Because the mirror was positioned exactly midway between the tablet and the screen, an upright virtual image of the display appeared in the plane of the digitising tablet.

The display consisted of a large grey square ( $200 \times 150$  mm) with nine white numbered squares on it measuring  $13 \times 13$  mm each. The distance between the centres of two neighbouring squares was 32 mm. A blue cursor spot of 4 mm in diameter was used to display the position of the hand, when necessary (i.e., on starting squares).

## Procedure

To familiarise the participants with the equipment, we illuminated the semi-silvered mirror from below at the outset of each experimental session. Both the display and the hand were then visible. We demonstrated to the participants that the point of the stylus and the cursor spot corresponded to every single position of the hand on the tablet. They were informed that their task would be to hit the centre of subsequently marked squares with the point of the stylus. The squares were marked in green. We instructed the participants that the stylus should not touch the tablet during the movement, i.e., we requested them to “jump” to the target. Within each trial, participants started on a square in the middle column (squares “2”, “5”, or “8”) and aimed at one of the neighbouring squares to the left or to the right side.

For example, starting square “2” was followed by target squares “1” or “3” only. Consequently, six pairs of starting and target locations existed. Movements from right or left squares to squares in the middle column were considered as a return to one of the three starting points and were not further exploited in the data analysis. When a starting square was marked, the blue spot indicated the position of the hand, so that the participants could easily find the adequate starting position. As soon as the stylus touched the virtual position of that square on the tablet, the blue spot was deleted and the colour of the square changed to red, indicating the correct starting position. After 100 ms, the square became white again and the subsequent target square lit up in green; 100 ms after the ballistic aiming movement was finished the next starting square was marked and so on. Note that the participants did not receive feedback about the trajectory or about

the end point of each critical movement. We instructed the participants to make the movements as quickly but as accurately as possible. Specifically, each participant was instructed to aim exactly at the centre of each target square. In addition, the participants were asked to prevent contact between tablet and forearm to ensure movement of the whole forearm and not only the hand.

Two blocks with 36 trials each were performed, i.e., each target square appeared six times per block. The order of the aiming movements was quasi-randomised. Half of the participants performed the first block with the right hand and the second block with the left hand. For the remainder the order was reversed. During the experiment the room was darkened except for the light from the upper screen. As a consequence, the hand was then invisible.

## Data reduction and analysis

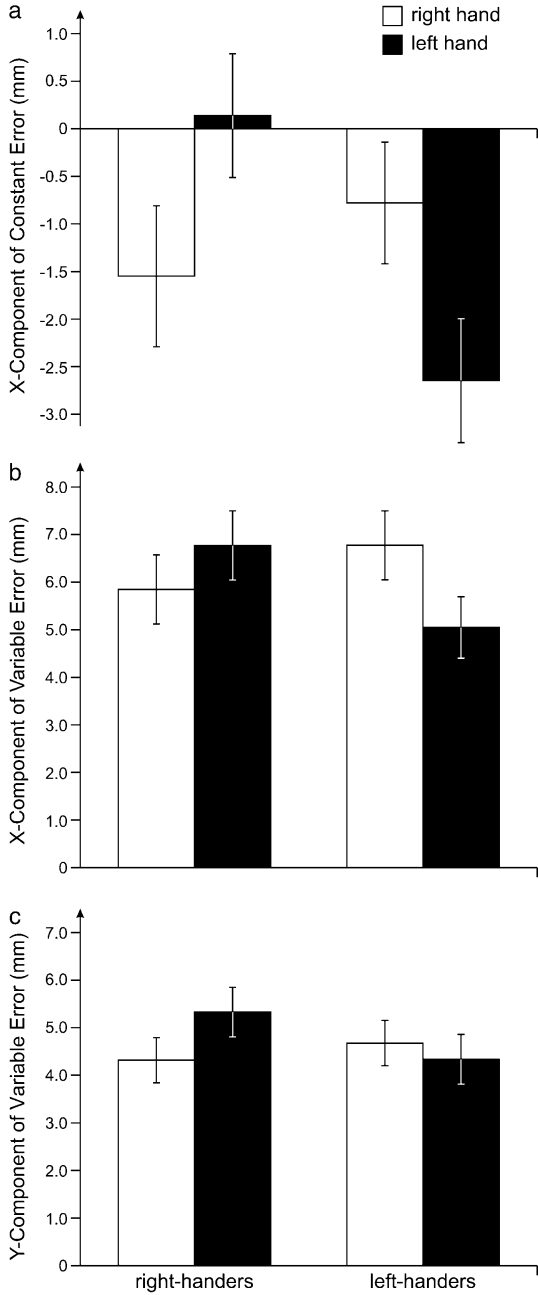
For each trial, the end position of the aiming movement was extracted from the collected data as coordinates on the tablet ( $x_{\text{end}}$ ,  $y_{\text{end}}$ ). For each individual participant, constant and variable errors were calculated for each position and block. Aiming errors in movement direction (x-component) and perpendicular to the movement direction (y-component) were analysed separately. Constant error was defined as Euclidean distance between the virtual position of the centre of a target square and the average end position of the participant on that square. The x-component of this distance was transformed so that negative values indicated undershoots and positive values indicated overshoots of the target. The variable error was defined as standard deviation of  $x_{\text{end}}$  or  $y_{\text{end}}$ , respectively.

Statistical comparisons were typically carried out with two-way Handedness (right-handers vs left-handers)  $\times$  Hand (right hand vs left hand) ANOVAs with repeated measures on the last factor. Post-analyses were performed with Student's *t*-tests. The criterion of significance was set to  $p < .05$ .

## RESULTS

### Constant error

The analysis of the x-component of the constant error yielded no main effects of handedness,  $F(1, 46) = 1.50$ ,  $MSE = 16.22$ , or hand,  $F(1, 46) = 0.03$ ,  $MSE = 7.24$ , but a significant interaction between hand and handedness,  $F(1, 46) = 10.47$ ,  $MSE = 7.24$ ,  $p = .002$ . Post-analysis for each handedness group revealed that right-handers tended to hit the targets more precisely with their left hand ( $M = 0.14$  mm,  $SD = 3.53$  mm) than with their right hand



**Figure 2.** Mean aiming errors (+SE) as a function of handedness and hand: (a) x-component of the constant error; (b) x-component of the variable error; (c) y-component of the variable error.

( $M = -1.55$  mm,  $SD = 3.20$  mm),  $t(23) = -2.12$ ,  $p = .045$ . Furthermore, the x-component of the constant error for aiming movements of the right hand significantly differed from zero,  $t(23) = -2.37$ ,  $p = .027$ , while it did not for movements of the left hand. The opposite was true for left-handers. They tended to undershoot the targets more with their left hand ( $M = -2.65$  mm,  $SD = 2.80$  mm) than with their right hand ( $M = -0.78$  mm,  $SD = 4.04$  mm),  $t(23) = 2.46$ ,  $p = .022$ . Moreover, only for the left hand of left-handers, the x-component of the constant error significantly differed from zero,  $t(23) = -4.62$ ,  $p < .001$ . The x-component of the constant error is depicted as a function of handedness and hand in Figure 2a. The analysis of the y-component yielded no significant effects of handedness,  $F(1, 46) = 1.58$ ,  $MSE = 15.66$ , or hand,  $F(1, 46) = 1.54$ ,  $MSE = 6.64$ , and no significant interaction between them,  $F(1, 46) = 0.59$ ,  $MSE = 6.64$ .

### Variable error

Analysis of the x-component of the variable error revealed no main effects of handedness,  $F(1, 46) = 0.22$ ,  $MSE = 17.53$ , or hand,  $F(1, 46) = 0.76$ ,  $MSE = 5.06$ , but a significant interaction of hand and handedness,  $F(1, 46) = 8.35$ ,  $MSE = 5.06$ ,  $p = .006$ . However, contrary to the x-component of the constant error, post-analysis only yielded significant differences between the right and the left hand for left-handers,  $t(23) = 3.08$ ,  $p = .005$ , but not for right-handers,  $t(23) = -1.27$  (see Figure 2b). The left-handers showed a smaller x-component of the variable error for their left hand ( $M = 5.05$  mm,  $SD = 2.96$  mm) than for their right hand ( $M = 6.78$  mm,  $SD = 3.96$  mm).

A significant interaction was also found for the y-component of the variable error,  $F(1, 46) = 4.39$ ,  $MSE = 2.50$ ,  $p = .042$ . Again there was no main effect of handedness,  $F(1, 46) = 0.25$ ,  $MSE = 9.45$ , or hand,  $F(1, 46) = 1.08$ ,  $MSE = 2.50$ . Post  $t$ -tests revealed that only for the right-handers was the y-component of the variable error marginally smaller when the movements were performed with the right hand ( $M = 4.32$  mm,  $SD = 2.21$  mm) as compared to the left hand ( $M = 5.33$  mm,  $SD = 2.71$  mm),  $t(23) = -2.02$ ,  $p < .055$ . No significant difference between the hands was found for left-handers,  $t(23) = 0.84$  (see Figure 2c).

## DISCUSSION

We conducted the present study to find out whether left-handers show similar asymmetries in the accuracy of aiming movements as compared to right-handers. It was supposed that an overall right hemisphere advantage for spatial planning in right- and left-handers would lead to pronounced



accuracy advantages of the left hand of left-handers. This was clearly not the case. While the variable error indicated that left-handers were more consistent when aiming with their preferred than with their non-preferred hand, the constant error indicated higher aiming accuracy in the non-preferred hand. Just like right-handers, left-handers significantly undershot the targets with their preferred hand, but they accurately hit the targets with their non-preferred hand.

Yamauchi, Imanaka, Nakayama, and Nishizawa (2004) found similar results in a transfer task. In their study, blindfolded participants performed a constraint criterion movement of 12 cm length with either the left or right hand and were subsequently requested to make test movements of equal, half, or double length with the contralateral hand. For both right- and left-handers, constant error of the non-preferred arm did not differ significantly from zero, while the preferred arm showed overshooting movements. However, the main purpose of their study was to examine interhemispheric transfer of kinaesthetic information about position in space. Therefore, the results were not interpreted as reflecting spatial planning accuracy of each hemisphere, but mainly as reflecting the direction of interhemispheric communication. In the light of the present study, it seems that their results can be better explained without referring to interhemispheric transfer.

The conclusions that can be drawn from our study (together with the results of other studies) are the following:

The constant error of aiming movements without visual feedback is lower for the non-preferred than for the preferred hand, i.e., right-handers hit the targets more precisely with their left hand (see also Guiard et al., 1983; Roy & MacKenzie, 1978) and left-handers hit the targets more precisely with their right hand (see also Yamauchi et al., 2004). These results suggest that the controller of the non-preferred hand draws on a more precise transformation from visually perceived targets into final postures of the moving limb (see also Sainburg, & Wang, 2002). As this transformation is essential in the stage of movement planning (Imamizu & Shimojo, 1995; Imamizu, Uno, & Kawato, 1995; Saltzman, 1979; Willingham, 1999), it can be concluded that the controller of the non-preferred hand plans movement end points more accurately than the controller of the preferred hand. The results of our study seem to contradict Boulinguez et al. (2001b), who found RT advantages for the left hand of left-handers and suggest an overall right hemisphere advantage for the spatial planning of movements. However, the origin of RT asymmetries may not be the same as that of accuracy differences between the hands. In a study of Barthemely and Boulinguez (2001), right-handed participants were requested to react to the same targets either with releasing a switch or with pointing to the targets. Both experiments revealed shorter RTs of the left hand, emphasising the role of visuospatial attention. However, the direct comparison between the RTs of

both experiments also showed a left hand advantage with regard to the specific cost of movement planning. Therefore, visuospatial attention might be more dominant in the right hemisphere, regardless of handedness, whereas spatial planning accuracy seems to be more closely connected to control of the non-preferred hand.

For the variable error the picture is not as clear. In our study, the variable error tended to be lower for the preferred hand. Guiard and colleagues (1983) found no significant difference between the hands as far as variable error is concerned, with only a slight advantage for the preferred hand at most. In visually guided aiming movements, Elliott and colleagues (1993) reported a significantly lower variable error for the preferred hand, while Goodale (1990) found no consistent difference between the hands. Therefore, the variable error is not able to reflect advantages of spatial planning accuracy. It rather seems to depend on movement execution than on movement planning.

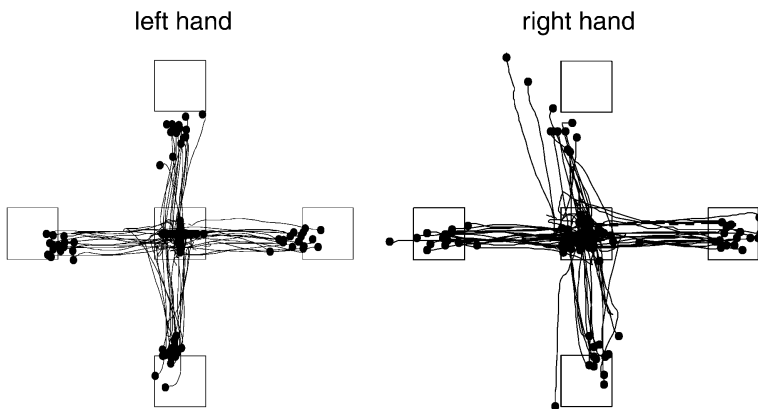
A more general suggestion for the present results might be that the controllers of the two hands are different with regard to the dominant form of movement control. It is a well-established fact that the preferred hand outperforms the non-preferred hand with regard to online control of the final corrective stage of aiming movements (e.g., Elliott et al., 1999; Mieschke et al., 2001; Todor & Cisneros, 1985). Therefore, the controller of the preferred hand might be more adapted for closed loop movement control, while the controller of the non-preferred hand seems to be better prepared for open loop movement control. This functional difference could, for example, be a direct result of more frequent supervision of the preferred hand, as compared to the non-preferred hand. Imagine, for example, threading a sewing needle. The focus is predominantly on the hand that holds the thread (which in most cases is the preferred one), not on the hand that holds the needle.

If accuracy differences between aiming movements of both hands really originate from the fact the hand–eye coordination is practised more often with the preferred hand, a person without clear preference for one hand should exhibit no such accuracy differences. We can present here the data from a 38-year-old ambidextrous woman, S.W., who draws with her left hand, but writes and throws with her right hand. As personally reported by S.W. and her mother, she has never been forced to switch her writing hand, neither at home nor at school. Furthermore, S.W. reports only minor inconveniences in switching hands in both writing and drawing. She exhibits high-level skills in fine motor control in both hands, as her hobbies are painting (with the left hand) and calligraphy (with her right hand). S.W. scores  $-2$  on the Lateral Preference Inventory (Coren, 1993), which indicates a slight preference for the left hand. However, she has never considered characterising herself as a left-hander. Figure 3 depicts the trajectories of

aiming movements without visual feedback that S.W. performed to four different targets, with each movement starting from the central square. The data were collected with the same apparatus as was used with the other participants in this study. However, as the target display was adopted from another unrelated experiment, the distance between the centres of the starting square and the target squares was 37 mm (instead of 32 mm for the other participants). S.W. performed 16 movements to each target square with either hand.

Surprisingly, S.W. showed a clear left-hander pattern in this task, i.e., aiming movements of the left hand were more consistent, whereas aiming movements of the right hand were more accurate. With the left hand, S.W. on average fell 8.10 mm short of the target centre, i.e., her movements only amounted to 78.1% of the optimal movement length, whereas with the right hand she produced a constant error of only  $-3.75$  mm (corresponding to 89.9% of the optimal movement length). By contrast, the variable error of the left hand tended to be smaller than that of the right hand (2.99 mm vs 5.02 mm in movement direction and 2.09 mm vs 3.11 mm perpendicular to the movement direction).

If asymmetries between aiming movements of both hands were in fact a result of different practice with both hands, S.W. should have displayed no or at least fewer such accuracy differences, because she has similar practical experience with both hands. However, the aiming asymmetries she displayed were about the same size as aiming asymmetries of strong left-handers. We therefore suggest that they might originate from innate functional asymmetries between the controllers of both hands rather than be acquired through practice. In most people, particularly in right-handers, hand preference



**Figure 3.** Movement trajectories of an ambidextrous person. The movements always started from the central square. No visual feedback of the hand was provided. The data reflect a typical left-hander pattern with consistent undershoots in the preferred hand.

might be the result of such functional asymmetries. Probably, the fact that despite strong performance asymmetries S.W. does not show a clear hand preference, indicates that she—like many other left-handers—conformed to the dextral society with regard to the main cultural skills (cf. Taniguchi et al., 1998).

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