

Hard and fast rules about the body: contributions of the action stream to judging body space

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Abstract Analogously to the visual system, somatosensory processing may be segregated into two streams, with the body constituting either part of the action system or a perceptual object. Experimental studies with participants free from neurological disease which test this hypothesis are rare, however. The present study explored the contributions of the two putative streams to a task that requires participants to estimate the spatial properties of their own body. Two manipulations from the visuospatial literature were included. First, participants were required to point either backward towards pre-defined landmarks on their own body (egocentric reference frame) or to a forward projection of their own body (allocentric representation). Second, a manipulation of movement mode was included, requiring participants to perform pointing movements either immediately, or after a fixed delay, following instruction. Results show that accessing an allocentric representation of one's own body results in performance changes. Specifically, the spatial bias shown to exist for body space when pointing backward at one's own body disappears when participants are requested to mentally project their body to a pre-defined location in front space. Conversely, delayed execution of pointing movements does not result in performance changes. Altogether, these findings provide support for a constrained dual stream hypothesis of somatosensory processing and are the first to

show similarities in the processing of body space and peripersonal space.

Keywords Action-perception · Left–right handedness · Lateralisation · Personal space · Body representation · Somatosensation

Introduction

In the visuospatial literature, there has been a long tradition of conceptualising processing as divided into two main pathways. Processing of visual information pertaining to the identity of an object is argued to be distinct from processing pertaining to the location of the same object (Ungerleider and Mishkin 1982). The two pathways proposed are the ventral and the dorsal stream. The former extends from the primary visual cortex and terminates in the inferior temporal cortex including V4, and the latter from the primary visual cortex to the posterior parietal cortex. According to the dual stream hypothesis, the ventral stream is dedicated to processing of perception and the dorsal stream to action (Milner and Goodale 1993; Milner and Goodale 2008). In addition, a temporal division between the streams may exist (Rossetti et al. 2003, 2005a), whereby the ventral pathway may be used particularly for the guidance of movements that are slow and represented throughout the movement sequence, and the dorsal pathway is primarily recruited for the guidance of fast, online-corrected movements (Ishihara and Imanaka 2008).

In addition to the traditional visual dual stream hypothesis, Dijkerman and De Haan (2007) propose a similar division for somatosensory processing. Here, somatosensory processing for the control of action is thought to be independent of processing pertaining to perception and

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memory. According to this model, the somatosensory analogue of the visual ventral stream runs from the anterior parietal cortex through the secondary somatosensory cortices (S2) and terminates in the insula. The analogue of the visual dorsal stream is suggested to extend from the anterior parietal cortex to S2 and the posterior parietal cortex. Importantly, and in contrast to the visual dorsal stream, Dijkerman and De Haan (2007) envisage this latter pathway as subserving somatosensory processing pertaining to *both* action and perception. Within this framework, different functions may be supported to a greater or lesser degree by the right and left hemispheres. While tactile (object) processing and semantic processing of the body appear to be more left-lateralised (Stoekel et al. 2004; Schwoebel and Coslett 2005), the right hemisphere appears to be of greater importance for the spatial configuration of one's own body (cf. Reed et al. 1996; e.g. Bisiach et al. 2004; Vallar et al. 1997; Committeri et al. 2007).

Dissociations between somatosensory processing pertaining to action and perception can be seen in blind touch, where a lesion affecting the perceptual stream results in deficits in the conscious recognition of tactile stimuli. Crucially, however, and presumably due to intact action stream functioning, the ability to correctly point to the location of tactile stimulation is preserved (Paillard 1999; Anema et al. 2009). The reverse deficit consisting of impaired pointing performance coupled with intact awareness of tactile stimuli has been reported in isolated cases of peripheral deafferentation (Paillard 1999) and left hemispheric stroke (Halligan et al. 1995).

Somatosensory information processing taking place in the action and perception streams can be characterised in a similar way to that of visual information processing. That is, a distinction with regard to the reference frame employed and with regard to the temporal dimension can be drawn. For example, a delay in the need to provide a motor response may result in significant performance decrements when pointing to the location of tactile stimulation in the aforementioned condition of blind touch, while immediate responses during or shortly after the occurrence of tactile stimulation are preserved (Rossetti et al. 2001). Conversely, following a delay, haptic performance may improve when neurologically normal participants are required to adjust the angle of a test bar to match a reference bar (Zuidhoek et al. 2003). This change in performance may also indicate a shift in the reference frame employed to solve the task. While immediate responses are likely to rely on a biased egocentric reference frame, delayed responses may benefit from a less biased allocentric reference frame (Zuidhoek et al. 2003; Kappers 2007).

To date, few studies have examined possible behavioural dissociations between somatosensory processing pertaining to action and perception in participants who are

free from neurological damage. In addition, most of the existing studies do not directly relate to (higher) somatosensory processing of the body itself but rather to (tactile or haptic) processing of external objects. Two notable exceptions (Marcel 2003; Kammers et al. 2009) are powerful in experimentally matching the perceptual and motor responses, but can only give limited information about everyday somatosensory processing due to their reliance on illusionary processes. In contrast, one task developed by Hach and Schütz-Bosbach (2010) may be particularly suited to studying the individual contributions of the putative streams without the employment of a somatosensory illusion. This task involves pointing movements directed to one's own body without the use of visual information. Using this task, the authors found right-handed participants to be affected by a spatial asymmetry when judging body space. Specifically, when requested to indicate the narrowest part of their waist and the widest part of their hip, right-handers pointed further away from the midsagittal plane in right hemisphere compared to left hemisphere—consistent with pseudoneglect for body space in right-handers, but not left-handers. Importantly, this asymmetry was absent in a perceptual task. The authors deduced that the asymmetry effect in right-handers may be driven by the somatosensory action stream.

However, it remains unclear to what extent the individual tasks in fact rely on processing of either somatosensory stream. The present study aims to address this question by implementing two experimental manipulations of the pointing task. First, two types of movement mode were realised. Right- and left-handed participants were required to either point to their body immediately or, in a different set of pointing movements, following a set delay. It was hypothesised that, if the body pointing task was exclusively driven by the action stream, there should be an asymmetry only in right-handers' body estimation and only when performing movements immediately following instruction, but not when performing delayed movements. In addition, due to the right-lateralised nature of spatial somatosensory functions, this asymmetry should be particularly pronounced when executing pointing movements using the left hand.

As a second manipulation of the task, two movement directions were included in order to necessitate the recruitment of an egocentric or an allocentric representation of participants' bodies. That is, participants were required to point at their own body either in backward-directed movements (egocentric condition) or in forward-directed movements at a forward mental projection of their own body. The latter condition, here termed 'allocentric', was hypothesised to rely on a more explicit, spatially transformed representation of the body which is centred on an external reference point. It was predicted that this

condition would counteract the asymmetry effect in right-handers if the pointing task was driven by the action stream. Conversely, the asymmetry would be evident in right-handers when pointing in a backward-directed movement. Again, asymmetry was hypothesised to be most pronounced for left hand pointing movements of right-handers. In contrast, performing pointing movements directed at a forward projection of one's own body should not be characterised by asymmetry as a perceptually driven mental spatial transformation of the body is presumably required.

Materials and methods

Participants

A total of 40 naïve, neurologically healthy participants (20 right-handers, 20 left-handers as categorised according to the Edinburgh Handedness Inventory, EHI, Oldfield 1971) provided written informed consent in accordance with the ethical standards of the 1964 Declaration of Helsinki and were paid for participating in a single session of about 60 min. A cut-off score of ≥ 60 on the EHI was used to classify participants as right-handers and of ≤ -60 for the classification of left-handers (see Table 1 for further participant characteristics).

Apparatus

Pointing movements were recorded by a Vicon motion capture system (Vicon—Oxford, UK, spatial resolution: 5 mm), an optical marker-based three dimensional motion

analysis system. Ten cameras were placed at approximately equal distances from the centre of the room. Participants were fitted with a total of 15 passive retro-reflective markers. These were located on the distal phalanges of the second finger on each hand, each wrist, on the right and left of the narrowest part of their waist, the widest part of their hips, as well as on the back of their pelvis. A pair of custom-built wooden frames was placed in the centre of the room and at a distance of 40 cm from each other. Each wooden frame contained a polystyrene screen measuring 50 by 100 cm. Participants were asked to stand directly behind the back screen. With the use of wooden dowels, the screen was individually adjusted to each participant's height. This resulted in the participants' body being concealed from the middle of their chest down, but allowed the participants to rest their forearms on the top of the screen, constituting the starting position for both the pointing and inactive hand in each trial. The screen held by the frame opposite was adjusted to the same height and served as a projection surface for forward-directed pointing movements (see Fig. 1a). The motion capture coordinate system was set up with the *x*-axis corresponding to a horizontal line running along the base of the back screen, the *y*-axis to a horizontal line at 90° to this, and the *z*-axis to a vertical line corresponding to the short side of the screen.

Data acquisition with a sampling frequency of 200 fps was controlled by Vicon Nexus software. At the start of each pointing movement, a digital signal was sent to a trigger panel, thus enabling the onset time of individual trials to be recorded along with the motion capture data. Performance was also videotaped by a digital camera (Sony HDR-HC9). Presentation® (Version 12.1, Neurobehavioral Systems, Inc.) was used to deliver auditory instructions and auditory cues to the participant through stereo speakers mounted in the right and left corners of the room.

Design and procedure

Any given trial began with a verbal pre-cue including the instructions of the movement direction (backward/forward), the hand used to execute pointing movements (right/left) and the landmark to which the pointing movement was to be directed (waist/hip) (e.g. 'Following the 'Go' signal, please indicate as quickly and accurately as possible in a backward-directed movement and with the use of your right hand the location of your left waist.'). Following the pre-cue, an auditory Go signal (frequency: 44,100 Hz, duration: 100 ms) was either given immediately, or a silent delay of 5,000 ms was given, after which the Go signal followed. Participants were instructed to point to the landmark as quickly and accurately as possible following the Go signal. Within the motion capture system, virtual

Table 1 Demographic characteristics of the total sample, right-handers (dextrals) and left-handers (sinistrals)

| | Total (<i>n</i> = 40) | Dextrals (<i>n</i> = 20) | Sinistrals (<i>n</i> = 20) | <i>P</i> |
|--------------------------------|---------------------------|------------------------------|--------------------------------|----------|
| Age | | | | |
| Mean (SD) | 23.90 (2.5) | 23.25 (2.1) | 24.55 (2.8) | .106 |
| Range | 20–30 | 20–27 | 20–30 | |
| Gender ratio (male: female) | 20:20 | 10:10 | 10:10 | 1.000 |
| Handedness | | | | |
| Mean (SD) | 3.42 (95.6) | 97.37 (5.4) | −90.53 (11.6) | <.001 |
| Range | (−100)–100 | 83–100 | (−60)–(−100) | |
| Body mass index | | | | |
| Mean (SD) | 22.37 (3.3) | 22.52 (3.4) | 22.19 (3.3) | .780 |
| Range | 18–33 | 18–33 | 19–29 | |

walls were set at the positions equivalent to those of the screens in the room. In the case of these ‘walls’ being touched by one of the markers, a non-audible sound signal was sent to Presentation, the experimental control program, to indicate the completion of a given trial. For trials in which participants were unable to fully execute the pointing movement within 1,000 ms (i.e. they did not reach the screen/virtual wall), an alarm signal was given. These trials were classified as failed and subsequently repeated at a random position in a given experimental block.

Participants were required to stand in a marked position behind one of the screens as described above. This resulted in the participant’s body being concealed from their view, thereby eliminating any informative visual feedback for the completion of the task. A short familiarisation with the motion capture environment followed and a brief practise block was administered. This practise block included immediate and delayed pointing movements directed at participants’ own bodies (backward condition) and to the screen in front of them (forward condition). Practise trials including pointing movements directed at both body outline landmarks (waist and hip) were included. Specifically, for the backward condition, participants were instructed to point at four points on the screen covering their body corresponding with the narrowest part of their right/left waist and the widest part of their right/left hip. For the forward condition, participants were instructed to point at a forward projection of these points on the screen facing them. That is, participants were asked to imagine that they were standing at the position of this second screen located 40 cm in front of their current position facing the same direction (i.e. right hip/waist on the right side of the screen; left hip/waist on left side of the screen).

Following this practise block, the experiment was conducted with the following factors administered block wise in a pseudo-randomised order; direction of movement (backward/forward), movement mode (immediate/delayed) and hand used to execute pointing movements (right/left). Hemisphere (right/left) and body outline landmark (waist/hip) were administered in a fully randomised manner. Three repetitions of each body outline landmark within each experimental block were included in the experiment, resulting in a total of 96 trials and a mean testing time of 20 min, including a short break between forward and backward blocks.

Performance measures

Data of three main dependent variables were collected. These variables included reaction time (RT), movement time (MT) and pointing bias. RT was defined as the time in ms between the sound of the Go signal and the start of the movement. MT was defined as the time between the start

and the end of the pointing movement. Start and end points of the movements were defined as movement of the right/left fingertip marker exceeding or falling below 50 mm per second on the x , y and z -coordinates, respectively. Pointing bias was defined as a deviation in mm between the end point of the right/left fingertip marker of the respective pointing movement and the position in space marking the body outline landmark (right/left waist/hip). For this measure, the intersection point between a straight line and a plane was calculated (Papula 1998) by applying the following formula with Matlab[®] (version 7, The MathWorks, Inc.).

$$rs = F + ((\text{dot}(n2, (BOL - F)) / \text{dot}(n2, n2)) \times n2)$$

where ‘ rs ’ refers to the position vector of the intersection point between a plane including the position vectors of the right and left hip (or waist) (here ‘ $a1$ ’ see Fig. 1b) and a straight line originating in the position vector of the (right/left) fingertip which is orthogonal to this plane (here ‘ $n2$ ’ see Fig. 1b). ‘ F ’ refers to the position vector of the right/left fingertip marker and ‘ BOL ’ to the plane including the right and left position vectors of the body outline landmark (waist/hip). Finally, ‘ $n2$ ’ is the normal vector orthogonal to the plane as described above (Papula 1998). Next, the distance between the intersection point ‘ rs ’ and the point in space at which the body outline landmark was located was determined and constituted the measure of bias. The x coordinate, as a measure of the deviation in the horizontal dimension, represented the key measure of pointing bias. Negative values indicated an undershoot, while positive values indicated an overshoot. In order to eliminate the influence of biomechanical constraints on the results, the z -coordinates were not taken into account for the calculation of pointing bias.

In addition, data from two kinematic variables were analysed. These included the movement peak velocity and total path length. Component velocities were directly exported from the Vicon system for each of the relevant frames of each trajectory. Movement peak velocity (PV) (in mm/s) was calculated by determining the resultant velocity of the component velocities along the three Cartesian axes (e.g. v_x , the velocity on the x -axis) through

$$\sqrt{(v_x^2 + v_y^2 + v_z^2)}. \text{ Path length (PL) denoted the total path}$$

which the right/left fingertip marker travelled between the point in time identified as the start of the movement (see above) and the point identified as the end of the pointing movement. Here, the distance between the right/left fingertip marker positions on pairs of consecutive frames along the trajectory was calculated by

$$\sqrt{((x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2)}.$$

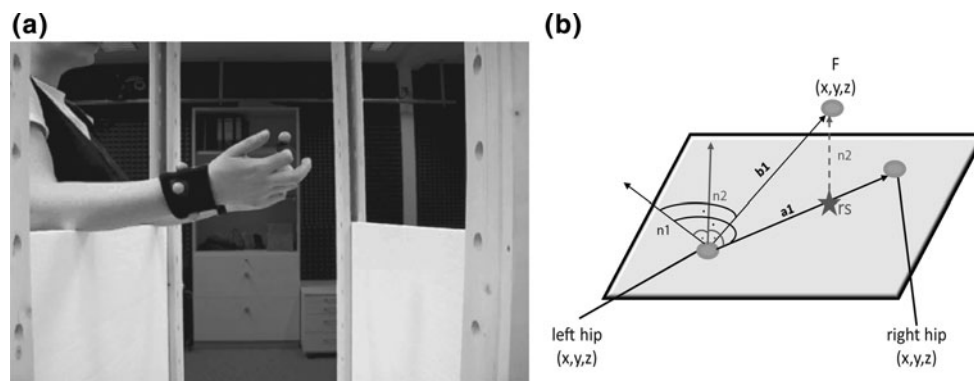


Fig. 1 **a** Experimental setup showing the starting position. Participants stood behind a screen adjusted to conceal their body from the chest downwards. A second screen was located 40 cm from this. **b** Schematic drawing of the three position vectors of interest (*left*

right hip and fingertip, 'F') and the direction and normal vectors (' $a/b1$ ', ' $n1/2$ ') used to calculate the intersection point ' rs ' between the plane (*grey*) and the normal vector ' $n2$ ' in line with the position vector 'F'

Analyses

Prior to the analyses of the individual performance measures, the raw data were screened for normality and homogeneity of variance. Trials with a RT smaller than 120 ms and those greater than 1,895.66 ms (mean RT + (3 SD)) as well as trials with a MT greater than 1,497.73 (mean MT + (3 SD)) were excluded as outliers from subsequent analyses. This resulted in a mean RT of 761.37 ms (SD 387.10), a mean MT of 727.75 ms (SD 256.66) and a trial retention of 90.33% (3,469 of a total of 3,840 trials). Subsequently, homogeneity of variance was determined by comparing the variance of each of the handedness groups within one performance measure. The largest variance was never greater than four times the smallest variance and skewness and kurtosis values did not exceed two times the standard error.

In a second step, trials that were initiated in a manner other than the instructions and corrected during the course of the trial and trials that were executed in a manner contrary to the instructions (e.g. right hand pointing movement in left hand trials; pointing movement directed at the right hemisphere in a left hemisphere trial) were excluded. Finally, trials during which the fingertip marker was lost for more than 50 frames (i.e. 250 ms) due to occlusion from the cameras through the experimental setup were excluded. The removal of all trials classified as invalid (645 trials) resulted in a final trial retention of 73.54% (2,824 of a total of 3,840 trials) across all participants and all experimental conditions. Vicon Nexus interpolation using the movement of anatomically connected markers as source (e.g. the finger root for the fingertip) was applied for any remaining sections of the movements where marker position was momentarily lost.

Separate analyses of variance (ANOVA) were carried out for each of the following performance measures; RT,

MT and pointing bias. A multivariate analysis of variance (MANOVA) was also run in order to control for type-one error rate. This analysis replicated the results of the ANOVA and is therefore not shown separately here. Following these analyses, post hoc analyses of the kinematic data (movement peak velocity and path length) were performed. Specifically, with the use of separate repeated measure ANOVAs, kinematic data from backward pointing movements were compared with the within-subjects factors handedness, hemisphere and hand used.

Results

Reaction time and movement data were analysed using analyses of variance (ANOVA) with handedness (right/left) as between-subjects factor and the following within-subjects factors; hand used (right/left), movement condition (immediate/delayed), movement direction (backward/forward), body outline landmark (waist/hip) and hemisphere (right/left). Overall, the results from these analyses showed evidence of the kinematic patterns common to unimanual pointing movements and of the experimental manipulations undertaken. For a summary of the results, refer to Table 2. Importantly, a significant three-way interaction between the factors hand used, hemisphere and handedness occurred only for movement time, but not for reaction times (see Table 2 for F and P -values). For right-handers, but not left-handers, there was a significant difference between the two hands pointing in right hemisphere, with longer movement times for the left hand (right-handers: $P = .002$; left-handers: $P > .05$) (see Fig. 2a).

For the key performance measure pointing bias, a third ANOVA with between-subjects and within-subjects factors as described above was performed. Pointing bias was defined as the horizontal distance (in mm) between the

Table 2 Summary of the results from the analyses of variance of the dependent measures reaction time (RT), movement time (MT; both reported in milliseconds), peak velocity (PV; in mm/s) and path length (PL; in mm) with the between-subjects factor handedness (right/left) and the within-subjects factors hand used (right/left), movement condition (immediate/delayed), movement direction (backward/forward), body outline landmark (waist/hip) and hemisphere (right/left)

| Measure | Main/interaction effect | <i>F</i> | <i>P</i> | Descriptives (mean; SE) |
|-----------|---------------------------------|----------|----------|--|
| RT (ms) | Movement condition | 21.94 | <.001 | Imm: 670.67; 32.25 Del: 858.93; 28.18 |
| | Landmark | 7.73 | .008 | Waist: 744.31; 23.32 Hip: 785.29; 24.32 |
| | Landmark*hemisphere | 5.32 | .027 | |
| | Hand used*hemisphere | 14.94 | <.001 | |
| | Handedness*hand used*landmark | 4.49 | .041 | |
| MT (ms) | Movement condition | 7.07 | .011 | Imm: 708.79; 15.43 Del: 744.51; 21.21 |
| | Landmark | 30.38 | <.001 | Waist: 701.12; 18.40 Hip: 752.18; 17.38 |
| | Direction | 22.79 | <.001 | Backw: 695.09; 20.36 Forw: 758.21; 16.44 |
| | Hand used*hemisphere | 45.01 | <.001 | |
| | Hand used*hemisphere*handedness | 5.12 | .029 | |
| PV (mm/s) | Handedness | 22.5 | <.001 | Right-handers: 1,134.09; 31.0 Left-handers: 978.410; 38.7 |
| | Hand used*hemisphere | 13.39 | <.001 | |
| PL (mm) | Handedness | 6.44 | .012 | Right-handers: 516.16; 10.98 Left-handers: 471.61; 13.7 |
| | Hand used*hemisphere | 296.6 | <.01 | |
| | Hand used*hemisphere*handedness | 6.76 | .01 | |

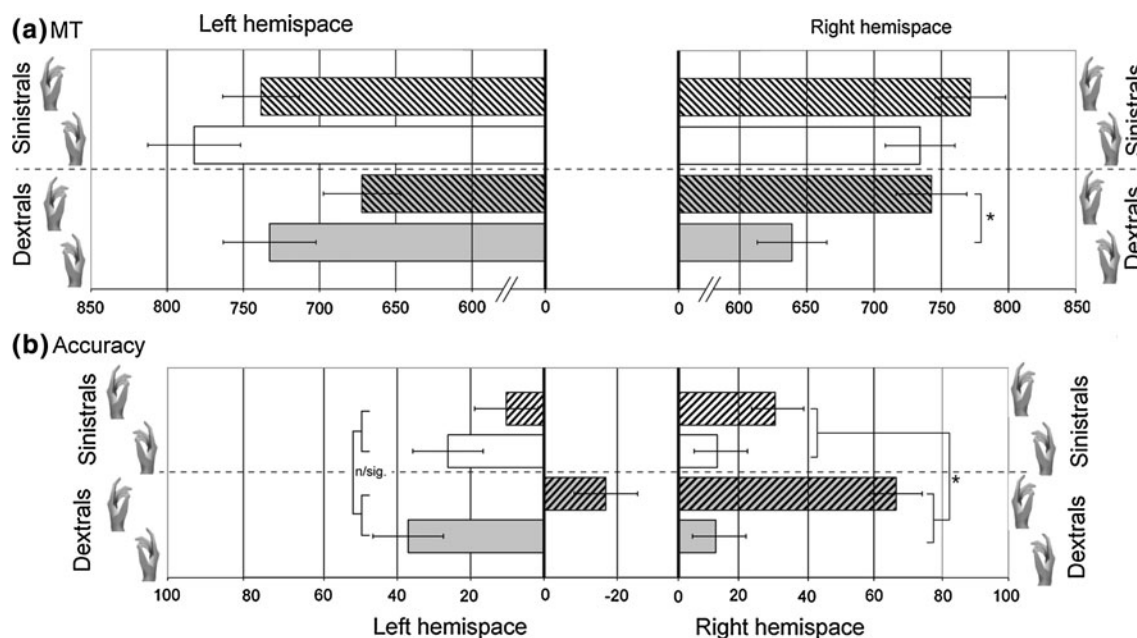


Fig. 2 a Mean movement time (ms) for left-handers (sinistrals; *top*) and right-handers (dextrals; *bottom*) as a function of the hand with which pointing was performed and the hemisphere to which pointing was directed. *Right hemisphere* depicted on the *right* of the figure and *left hemisphere* on the *left*. **b** Mean deviation from veridical location of the body outline landmarks (in mm) for sinistrals (*top*) and dextrals

(*bottom*) as a function of the hand with which pointing was performed and the hemisphere to which pointing was directed. *Right hemisphere* depicted on the *right* of the figure and *left hemisphere* on the *left*. Negative values represent an underestimation and positive values an overestimation. * denotes significant difference ($P < .01$). Error bars represent standard error

location of the finger tip marker at the end of the pointing movement and the location of the marker attached to the waist/hip. Positive numbers indicate an overshoot and negative numbers indicate an undershoot. A significant main effect of direction of movement was found ($F(1, 38) = 15.58, P < .001$), with greater errors shown in pointing movements directed at front space (mean 31.71, SE 4.48) compared to backspace (mean 12.87, SE 4.19) (see Fig. 3). A second main effect of hemispace ($F(1, 38) = 5.84, P = .021$) indicates larger errors in right hemispace (mean 29.92, SE 4.47) compared to left hemispace (mean 14.66, SE 5.12) (see Fig. 3). In contrast, the effect of movement condition (immediate vs. delayed) on pointing bias only approached significance ($F(1, 38) = 2.93, P = .078$; immediate: mean 19.75, SE 3.85; delayed: mean 23.93, SE 3.62).

Crucially, there was a significant interaction between hemispace and handedness ($F(1, 38) = 4.21, P = .040$), indicating that pointing errors differed for right-handers and left-handers in the right and left hemispaces. Post hoc pairwise comparisons show that for right-handers, there is a significant difference between pointing bias in right and left hemispaces. Right-handers' errors in right hemispace (mean 39.31, SE 6.40) were significantly larger compared to both left hemispace errors (mean 11.10, SE 7.33) and left-handers' pointing errors in right hemispace (mean 20.52, SE 6.23) (see Fig. 2b). In contrast, there was no significant difference between the bias displayed by left-handers in right and left hemispace ($P > .10$). A second two-way interaction between hand used and hemispace also occurred ($F(1, 38) = 25.83, P < .001$). Pointing to contralateral space produced larger errors compared to pointing to ipsilateral space for both hands (all $P_s < .05$, Bonferroni corrected).

A number of three-way interactions also occurred. First, there was an interaction between the hand that was used to

perform the task, the body outline landmark to which pointing was directed and the pointing direction (forward/backward) ($F(1, 38) = 9.06, P = .005$). Pointing in a forward-directed movement regardless of which hand was used and which body outline landmark pointing was directed at always resulted in larger errors (all $P_s < .05$, Bonferroni corrected) except for pointing movements executed with the left hand directed at the hip. For these trials, the difference between backward and forward pointing errors followed the same pattern, but failed to reach significance ($P > .10$). Second, hand used interacted significantly with body outline landmark and hemispace ($F(1, 38) = 11.84, P = .001$). This interaction stems from the overall pattern of contralateral pointing movements producing larger errors compared to ipsilateral pointing movements (as described above; all $P_s < .01$, Bonferroni corrected) except for trials in which the right hand was pointing to the hip ($P > .10$).

Finally, the interaction between hand used and hemispace was further and separately significantly modulated by the factors direction ($F(1, 38) = 46.85, P < .001$), condition ($F(1, 38) = 18.73, P < .001$) and handedness ($F(1, 38) = 7.62, P = .009$). This first three-way interaction with the factor direction indicates that the general pattern of larger errors for contralateral pointing movements is not equally strong for both directions. Post hoc pairwise comparisons show that contralateral pointing errors were larger compared to ipsilateral pointing errors for forward-directed movements (all $P_s < .05$, Bonferroni corrected), but this pattern failed to reach significance for backward-directed movements (all $P_s > .10$). The second three-way interaction with the factor condition shows that the bias for contralateral pointing trials was unaffected by the movement mode (immediate/delayed) (all $P_s > .10$) whereas ipsilateral pointing trials differed for immediate and delayed movements (all $P_s < .05$). However, the

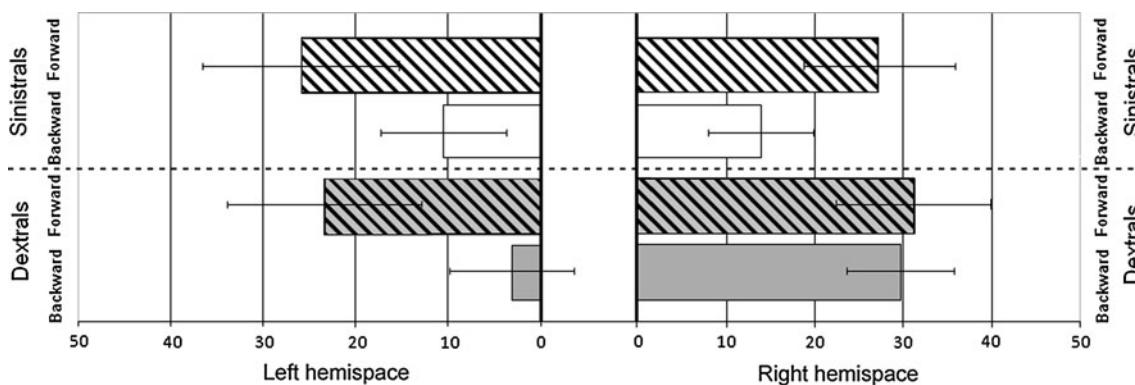


Fig. 3 Mean deviation from veridical location of the body outline landmarks (in mm) for sinistrals (*top*) and dextrals (*bottom*) as a function of the hemispace to which pointing was directed and the pointing direction. *Right hemispace* depicted on the *right* of the figure

and *left hemispace* on the *left*. *Solid bars* represent backward-directed movements and *dashed bars* movements directed to front space. Negative values represent an underestimation and positive values an overestimation. *Error bars* represent standard error

means did not show a consistent trend. For example, immediate ipsilateral pointing trials with the left hand showed larger errors compared to delayed ipsilateral pointing trials, while the reverse pattern occurred for the right hand (i.e. smaller errors in immediate ipsilateral trials compared to delayed ipsilateral trials).

Importantly, right-handers' pointing bias (all P s < .001, Bonferroni corrected) differed as a result of the hemispace to which pointing was directed and the hand that was used to perform the pointing but for left-handers, it did not (all P s > .10). For right-handers, the mean difference between right and left hand was more than three times greater (mean difference 54.18, SE 11.05) than that for left-handers (mean difference 16.70, SE 11.05). In addition, post hoc pairwise comparisons show that for right-handers, there was a significant difference in pointing to the right and left hemispace using the left hand (P < .001, Bonferroni corrected) (see Fig. 2b). Similarly, the difference between right and left hemispace pointing for right-handers using the right hand approached significance (P = .07, Bonferroni corrected). In contrast, for left-handers, no significant differences were found between right and left hemispace pointing for either hand (all P s > .10) (see Fig. 2b).

In light of the results showing that movement time, but not reaction time differences between right- and left-handers parallel the pointing bias results, two post hoc repeated measure ANOVAs were calculated. These analyses compared the effect of the factors handedness, hemispace and hand used on both movement peak velocities (PV) and path length (PL). Due to the absence of a handedness by hemispace interaction in the forward pointing condition (see Fig. 3), post hoc analyses were restricted to the backward pointing condition. There was a main effect for the factor handedness for PV as well as for PL, indicating the presence of kinematic differences in the pointing movements of the two handedness groups. Right-handers exhibited higher PVs and longer PLs compared to left-handers. The results of these post hoc analyses are summarised in Table 2 (see also Figs. 4, 5).

Discussion

It has been suggested that, similar to visual processing, somatosensory processing can be divided into an action and a perception stream. Experimental studies testing this hypothesis by investigating the somatosensory processing of the body *per se* and further by including populations free from neurological damage are rare, however. The present study aimed to manipulate the contributions of the purported processing streams to the solving of a task pertaining to the spatial representation of our own body. To this end, participants were requested to perform pointing

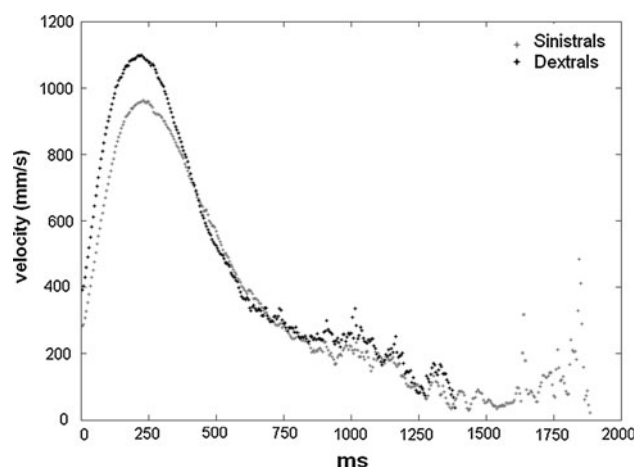


Fig. 4 Mean peak velocity (in mm/s) for left-handers (sinistrals, grey) and right-handers (dextrals, black) as a function of time for backward-directed movements combined for movement condition (immediate/delayed), body outline landmark (waist/hip) and hemispace (right/left)

movements indicating the horizontal extent of their body in the right and left hemispaces. Pointing movements were either executed immediately following instruction or after a set delay. Further, the direction of pointing was varied with half of all movements directed backward at the participant's own body and half directed forward at a (mental) projection of the participant's own body.

The results show a significant bias only in backward-directed pointing movements in right-handers' estimation of their body space in right hemispace compared to left hemispace. This confirms two points. First, it replicates our earlier results (see Hach and Schütz-Bosbach 2010) and extends existing research showing a bias in right-handers' performance on spatial tasks across different sensory modalities (for a meta-analysis, see Jewell and McCourt 2000). In line with the current finding, a number of studies also show that, compared to left-handers, right-handers have decreased access to right-hemispheric functions such as bodily representations. For example, right-handers have been shown to display a disadvantage in the recruitment of the spatial properties of their own body (Christman et al. 2007; Linkenauger et al. 2009) as well as the update of the representation of their own body (Niebauer et al. 2002).

Second, the lack of asymmetry in right-handers' forward-directed pointing movements shows that laterality effects exert less influence on more allocentric body representations. That is, in contrast to the implicit egocentric representation afforded by backward-directed movements (Rossetti 1998; Rossetti et al. 2005b), the representation afforded by forward-directed movements may be more explicit, cognitively mediated and ventrally driven (see also Blanke et al. 2005). The classical distinction between body schema and body image (Paillard 1999, 2005), where

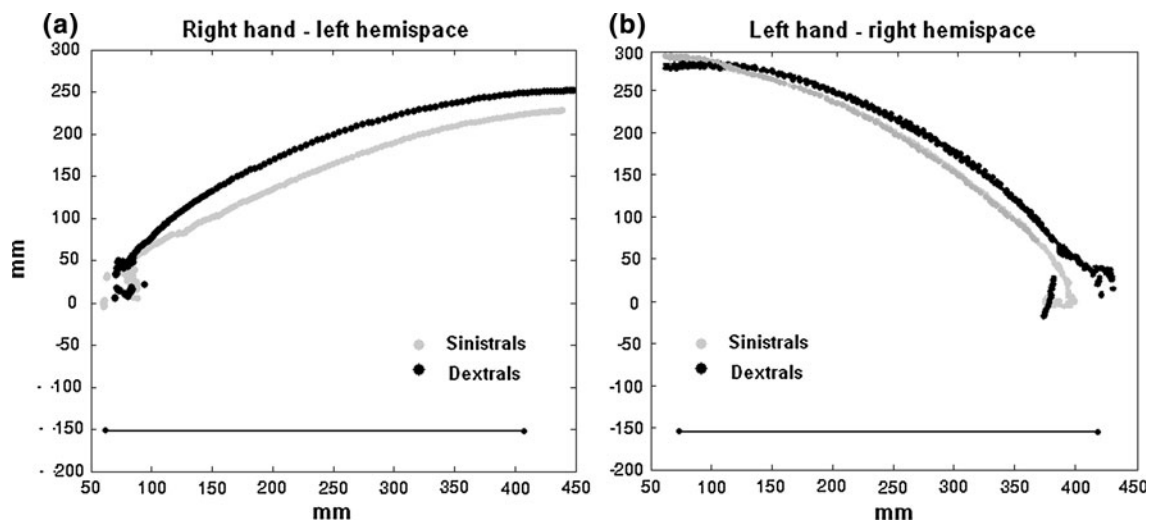


Fig. 5 Mean movement path for backward-directed pointing movements of right-handers (dextrals, *black*) and left-handers (sinistrals, *grey*) combined for both body outline landmarks (waist/hip) depicted at the *bottom* of the figure, and movement modes (immediate/delayed). For illustrative purposes, the location of *right* and *left* body

outline landmarks are aligned and normalised in space. **a** Mean path of the *left hand* pointing at *right hemisphere* (movement trajectory starts at top *right* of figure and ends on *left*). **b** Mean path of the *right hand* pointing at *left hemisphere* (movement trajectory starts at top *left* of figure and ends on *right*)

a backward-directed movement would be supported by the body schema to a greater extent while forward-directed movements would be supported by a representation of the body in terms of a body image, maps well onto this finding. The dual stream hypothesis of somatosensory processing also terms the former a product of the action and the latter a product of the perceptual stream (Dijkerman and De Haan 2007).

Support for this dissociation stems from the neuropsychological literature, where either of these representations can be affected following focalised lesions, as for example in egocentric and allocentric tactile neglect (Marsh and Hillis 2008). Egocentric and allocentric (body) representations may also influence each other, as can be seen in patients affected by blind touch whose pointing performance can be reduced to chance levels when requested to elaborate on tactile stimulation (i.e. by indicating the location of the stimulation on a line drawing of an arm) (Rossetti et al. 1995; Rossetti 1998). In short, depending on whether the body is part of the action system or the perceptual object itself (De Vignemont et al. 2005), different representations may be employed to a greater or lesser extent (Kammers et al. 2006). One way of manipulating this balance within the present paradigm may lie in a change of the direction of pointing.

Moreover, the present study shows that right-handers' overestimation in right hemisphere was mainly driven by the left hand. This is consistent with greater right-hemispheric dominance for spatial functions in right-handers (for a meta-analysis, see Vogel et al. 2003) as well as a right-hemispheric dominance of the representation of one's

own body (e.g. Bottini et al. 2002; Blanke et al. 2004; Ehrsson et al. 2004; Committeri et al. 2007; Vallar and Ronchi 2009). Analogous to our results, studies relating to body representations in neurologically normal participants have reported a special role of the left hand. For example, the left hand may be more susceptible to the rubber hand illusion (Ocklenburg et al. 2010).

Several factors speak against an alternative interpretation of this effect in terms of a general non-dominant hand disadvantage in right-handers. First, intermanual accuracy differences for right-handers have only been reported for non-ballistic movements (e.g. Roy and Elliott 1986; Carson et al. 1993) and not for ballistic movements (Steingrueber 1975; Elliott et al. 1994; Sainburg and Kalakanis 2000). Further, intermanual accuracy differences for the former type of movement have been attributed to differences in the utilisation of sensory feedback (for a review, see Goble and Brown 2008a) with the right hand relying on visual and the left hand on proprioceptive feedback to a greater extent (e.g. Goble and Brown 2008b, 2009). Thus, with the use of the present paradigm, there should be a left hand *advantage* rather than a disadvantage. Second, kinematic studies examining right-handers' dominant and non-dominant hand performance report differences in trajectory curvatures and muscle control only (e.g. Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002). Importantly, these differences do not result in a significant intermanual difference in the total path length, as can be seen in the present study.

Crucially, our analyses of the measures reaction time and movement time show the absence of a speed-accuracy

trade-off. Rather, the difference in pointing bias is mirrored only in movement times. Significantly greater peak velocities and longer path lengths for pointing movements executed by right-handers accompanied these results. The former is suggestive of a lesser degree of online control throughout movement execution (e.g. Ketelaars et al. 1997; Desmurget et al. 2004; Cohen et al. 2009). The latter is consistent with increased availability of sensory feedback for left-handers. This is well illustrated when visualising contralateral pointing movements (see Fig. 5) where left-handers' movements come closer to a line connecting initial and final positions, while right-handers' movements more prominently display the curvature characteristic of horizontal and vertical arm movements (Atkeson and Hollerbach 1985; Desmurget et al. 1999; Pozzo et al. 2002).

One last main finding of the present study concerns the general pattern of overestimation in participants' performance of the pointing task. Both right-handers and left-handers overestimated the dimensions of their own body along the horizontal axis in backward-directed and forward-directed movements. Similarly, Gurfinkel and Levick (1991) report a systematic distortion of the body representation when participants were asked to point to selected joints while their body was covered from view. A general overestimation of the width of one's own body is consistent with the finding of a contracted and broadened implicit representation of one's own hand (Longo and Haggard 2010). However, while the characteristics of the implicit hand representation show some similarity with the primary somatosensory representation, it remains unclear to what extent this is true for the implicit representation of the trunk that may have been accessed in the present study. Future studies could examine whether the horizontal overestimation reported with this paradigm is accompanied by a corresponding contraction of the perceived vertical distance between the right/left waist and hip.

The results discussed thus far are in contrast to those of the second experimental manipulation performed as part of the current study. Altering the movement mode, that is, whether participants performed pointing movements immediately following instruction or after a set delay, did not result in any significant differences between the participant groups and right and left hemispaces. It was hypothesised that, if the pointing task was exclusively driven by the action stream, the introduction of a delay between the instruction and execution of the pointing movement should result in the elimination of the asymmetry effect. Instead, the asymmetry effect was shown in right-handers' pointing performance regardless of the movement mode. We suggest the following possible explanations for this finding.

First, this finding may reflect modality-specific differences. In the visual domain, a manipulation of the dorsal and ventral contributions to the solving of a task is easily operationalised since the time window during which visual feedback is present can be manipulated without any difficulty. However, for somatosensory feedback, such manipulations are less easily possible because kinaesthetic and proprioceptive feedback cannot ever be completely eliminated. Therefore, it may be that the null finding with regard to the manipulation of movement mode results from the constantly present somatosensory feedback available to our participants throughout the entire experiment. According to the 'real-time' hypothesis, for example, ventral stream activity only supports processing of a target which is not (visually) represented in the physical environment (Westwood and Goodale 2003). Such a distinct separation is less possible when investigating somatosensory processes.

Second and as noted above, somatosensory processing as envisaged in the model by Dijkerman and De Haan (2007) may not be as strictly divided into two streams as it has been suggested by some investigators for visual processing. Within the somatosensory dual stream hypothesis, the posterior parietal cortex subserves processing of bodily information for both action and perception. Other similar models also envisage considerable interplay between the respective streams (Longo et al. 2010). In addition, further experimental studies of somatosensory processes suggest a weighting of the input from the action and perception stream depending on the specific situation at hand (e.g. Kammers et al. 2009; Schütz-Bosbach et al. 2009). Future studies may aim at systematically lengthening the delay between instruction and movement execution in order to decrease the influence of proprioceptive and kinaesthetic cues from one pointing movement on the next. Notwithstanding the absence of an effect of the movement mode manipulation, the finding of an asymmetry effect in right-handers' estimation of body space and the finding of a modulation of this effect through a change of the pointing direction remains strong.

In sum, somatosensory processing pertaining to one's own body may be supported by the action or perception stream to a greater or lesser extent depending on the task at hand. Results from the present study utilising the body pointing paradigm highlight similarities and differences between visuospatial and somatosensory processing pertaining to a spatial representation of our own body.

Introducing a delay between the instruction and the execution of a pointing movement, as commonly operationalised for visuospatial tasks, does not result in performance changes for the present task. However, the presence of a systematic bias for body space in right-handers could be confirmed. The present results further show that this bias particularly affects actions towards one's own body in egocentric coordinates rather than actions towards a more allocentric representation of one's own body.

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