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The handedness of postural fluctuations

R. Balasubramaniam *, M.T. Turvey

Department of Psychology, Center for the Ecological Study of Perception and Action, University of Connecticut, 406 Babbidge Road, Storrs, CT 06269 1020, USA

Abstract

In two experiments we investigated whether the dynamics of standing upright were lateralized. The postural task of Experiment 1 introduced a lateral bias of attention; the postural task of Experiment 2 did not. In Experiment 1, six left-handed and six right-handed participants passively held a laser pointer at the side of the body in either the left or right hand. Successful pointing at targets that varied in distance and size required minimizing the body's medio-lateral (ML) sway. Sway variability, in the range of 2.8–5 mm, was smaller in the anterior–posterior (AP) direction (of relevance to keeping upright) and larger in the ML direction when the pointer was on the preferred rather than non-preferred side. In Experiment 2, six left-handed and six right-handed participants maintained quiet stance while visually fixating a target. Variability of ML and AP sway changed in the same way with difficulty of the precision aiming task and did so independently of handedness. Discussion focused upon the possible mechanism of postural lateralization and the nature of the tasks by which such lateralization is revealed. © 2001 Published by Elsevier Science B.V.

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* Corresponding author. Present address: Centre de Recherche, Institut de Readaptation, University of Montreal, 6300 av Darlington, Montreal, QC H3X 253, Canada. Tel.: +1-514-340-2078; fax: +1-514-340-2154.

E-mail address: mahavishnu@sympatico.ca (R. Balasubramaniam).

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1. Introduction

The concept of handedness has shaped most considerations of the functional asymmetry or laterality of the human movement system. To a significant degree, the privileged status of handedness has arisen because hand preference is a relatively obvious feature of a person's behavior and because, more formally, a person's preference for hand use can be assessed in straightforward ways by either a questionnaire or a battery of performance tests. It is noteworthy that the common denominator of the different questionnaires directed at laterality are queries about which hand carries out specific dexterous activities, such as writing or catching a ball.

Despite the theoretical and experimental preoccupation with handedness as the hallmark of motor laterality, it has not escaped notice that movements of a coarser nature than those exhibited by hands, such as the movements involving the trunk, may be lateralized. In respect to the skills defined over the body as a unit – for example, riding a bicycle or standing upright – Geschwind and Galaburda (1987, p. 76) comment that:

> Since the latter type of skill is not *obviously* lateralized, it has not entered into studies of cerebral dominance. Since muscles of both sides of the trunk are used in these activities in coordination with limbs on both sides, it may seem odd to postulate dominance for one of them. Even if they were controlled predominantly from one hemisphere, it would be difficult to determine the leading half of the brain by either questionnaire or tests of performance.

Geschwind and Galaburda (1987) argue that one should not be surprised by the possibility that lateralization holds true for full body movements that depend on bilateral activation. In support, they note that speaking entails bilateral innervation of articulatory and respiratory muscles and yet it is the case that speaking is very much the product of one cerebral hemisphere (typically the left). Indeed, Geschwind and Galaburda highlight that speaking may be more symmetrical than many trunk movements, citing anecdotal evidence that ice-skaters find it easier to execute turns in one direction than in the other.

Lateralized control of full body behavior may originate in the same cerebral hemisphere as the control of manual behavior (Geschwind & Galaburda, 1987). This is more likely to be the case for persons with so-called standard dominance – strong left hemisphere dominance for language and handedness – than in persons who exhibit a laterality pattern that differs from the standard form, so-called anomalous dominance (Annett, 1985; Geschwind & Galaburda, 1987). Accordingly, we might expect that any asymmetry in postural behavior would reflect hand preference. A common cerebral bias for the two types of asymmetric activity does not mean, however, that they are manifest through common neural mechanisms. Geschwind (1975) suggests that their supportive neural structures are sufficiently different to warrant their recognition as distinct systems of motor control and motor learning that he labels *pyramidal* and *axial*. The former label is for the system that subserves manual skills and the latter label is for the system that subserves body skills.

It is important to note that Geschwind and Galaburda's conjecture on the generalization of movement asymmetry to the body as a whole is rare in the literature on the control and coordination of movement. To the contrary, if the idea is considered, it is typically dismissed as unlikely. One of the most comprehensive accounts of the functional levels and design of biological movement systems is that provided by Bernstein (1996). In this account, symmetry rather than asymmetry characterizes the movements constructed at the functional levels of tone (Level A), muscular–articular links (Level B), and space (Level C). Lateral asymmetry is restricted to manual activities that typify the level of actions (Level D), the level at which sequences of distinct movement patterns, usually involving objects, occur. With respect to the movements associated with the Levels A, B, and C, Bernstein (1996, p. 152) remarks: "All these movements are perfectly symmetrical: their right side is equivalent to their left side." The impetus for the latter point of view is most surely the absence of any obvious observable differences of a systematic nature between the two sides of the body during movements that involve a unitary coordination of trunk and limbs. We suspect that rather special experimental settings may be needed to make the asymmetry postulated by Geschwind and Galaburda obvious.

In the present research we focus upon one particular, commonplace behavior of the body as a unit. Specifically, we focus upon standing upright in the absence of forces that might compromise the posture. This particular behavior, perhaps more than any other, would seem to be least disposed to asymmetric control, that is, least likely to conform to Geschwind and Galaburda's conjecture. Consequently, finding support for the conjecture in this instance would be especially compelling. The challenge is to identify the experimental conditions that are most likely to reveal the expected asymmetry of standing upright.

From Geschwind's (1975) claim that pyramidal and axial systems are often lateralized in the same way, we can assume that one of the required conditions is handedness. The experiment should include both right-handed and left-handed participants because the organization of postural control should differ between them, thereby making the asymmetry more evident. A second condition follows from the claim that evidence for laterality is more likely to be found in situations that require or encourage asymmetries in attention and/or effort (e.g., Amazeen, Amazeen, Treffner & Turvey, 1997; Kinsbourne, 1995; Peters, 1994; Riley, Amazeen, Amazeen, Treffner & Turvey, 1997). Simply standing upright involves a seemingly even distribution of effort and attention across segments of both sides of the body and across both primary directions of sway (medio-lateral and antero-posterior). By the preceding claim, we can assume that what is needed is a task superimposed on standing upright that breaks the normal attentional symmetry of standing upright. Specifically, what is needed is a task that is biased to one or the other side of the body and to one or the other direction of sway.

A task of the preceding kind was recently investigated by Balasubramaniam, Riley and Turvey (2000). It was inspired by precision aiming tasks such as archery and rifle shooting. Participants stood with the right hand holding a laser pointer to the side of the upright body with the arm parallel to the body's longitudinal axis and the hand immobile against the thigh. Maintenance of the pointer on a target was achieved by keeping the body still. The task was performed in two orientations of the body's coronal plane to the target. In the parallel orientation, medio-lateral (ML) sway had to be minimized; in the perpendicular orientation, antero-posterior (AP) sway had to be minimized. It was found that in the parallel orientation, ML sway decreased and AP sway increased with difficulty of the precision task as manipulated through target distance and target size. The pattern reversed in the perpendicular orientation. A major conclusion was that a postural organization for upright standing and aiming (as in archery) entailed two independent postural subsystems whose fluctuations are (a) negatively correlated in magnitude, and (b) different in the fine structure of their time correlations as revealed through recurrence analysis (Riley, Balasubramaniam & Turvey, 1999; Webber & Zbilut, 1994).

The measure of postural fluctuations used by Balasubramaniam et al. (2000) was the variability in center of pressure (COP). The COP is a measure of the vertical ground reaction vector and is equal and opposite to a weighted average of all downward forces acting between the feet and the ground. It is related to, but not identical with, the center-of-gravity vector. The outcome of Balasubramaniam et al.'s investigation was consistent with the understanding that two independent muscular subsystems are primarily responsible for COP. These subsystems are plantar flexion/dorsi flexion at the ankle and adduction/abduction at the hip (Winter, Prince, Frank, Powell & Zabjek, 1996). Experiments in quiet, unperturbed standing have shown that, when the feet are side-by-side, the two subsystems are responsible, respectively, for motions of the COP in the AP and ML directions (Winter et al., 1996). If there is asymmetry in upright standing, as expected from Geschwind and Galaburda's conjecture, then it might be realized as a bias in the deployment of the ankle and hip subsystems governing COP.

2. Experiment 1

In Experiment 1 we combined the two conditions that seem to be required for revealing laterality in upright standing, namely, handedness and attentional asymmetry. Specifically, left-handed participants and right-handed participants executed postural control of precision aiming with a laser pointer on the left side or the right side of the body. Analyses focused upon the patterning and relative magnitudes of COP fluctuations in the ML and AP directions as a function of target parameters and handedness. In the present experiment, a bias in the deployment of the ankle and hip subsystems should show up as a difference in the patterning of AP and ML fluctuations by left-handed participants and right-handed participants.

2.1. Method

Participants. The participants in the experiment were six left-handed and six right-handed students from the University of Connecticut. (Seven of the participants were female.) Handedness was by personal report confirmed by answers to the questions of which hand was used for throwing and which foot was used for kicking. The participants ranged in age from 18 to 35 years (mean of 24.7 years), in weight from 44.6 to 92 kg (mean of 71.7 kg), and in height from 157 to 195 cm (mean of 169.2 cm). None of the subjects reported recent injuries at the time of the experiment.

Apparatus, data collection and reduction. COP data were collected using a Kistler force platform (Type 9281B) and a Kistler charge amplifier (Type 9865) set to 10 000 pC. The AP and ML fluctuations were sampled at a rate of 100 Hz, yielding a total of 3000 data points per 30 s trial. Data were collected on a microcomputer using Force Analysis Software System (FASS) digitizer software (ESI Technologies, OH).

Stimuli. The target was a white square of 36 cm^2 at the center of four equal black squares each of area 9 cm^2 on a sheet of paper 21.6 cm $\times$ 27.9 cm, each black square was separated by 6 cm. The target was affixed to a plane surface located at a distance of 2.2 or 3.3 m from the participant. At these distances, the square target region subtended vertical/horizontal visual angles of 0.78°, and 0.52°, respectively. An index of difficulty (ID) was defined as the ratio of twice the target distance to the target size.

A handheld laser pointer was used to project a horizontal arrow onto the target. The area covered by the horizontal arrow increased with target distance – approximately 12 and 18 cm^2 at 2.2 and 3.3 m, respectively. The vertical and horizontal visual angles subtended by the arrow at these distances were 0.52° and 0.39°, and 0.39° and 0.35°, respectively.

Procedure. Participants stood on the force platform in a dimly lit room with all surrounds visible. They stood with arms by the side holding a laser pointer in the right or left hand. The hand was held against the thigh. Each trial began with the participant aligning the laser pointer with the target. The target was oriented in a plane parallel to the coronal plane of the body and displaced off-center to be approximately in line with the participant's hand. To achieve the required alignment, the participant merely had to adjust the hand position to orient the laser beam. As in Balasubramaniam et al. (2000), we opted for voluntary immobility of the hand rather than affixing the hand to the thigh by tape (for example). We did so in order to (a) facilitate the comfort of the participants, and (b) allow a simple means (namely, hand rotation) by which any participant, regardless of his or her height relative to the fixed target height, could direct the laser beam onto the target prior to the start of a trial. Once the beam and target were aligned, the hand was to be kept immobile. Participants were instructed to keep the laser arrow on target by simply "standing still".

A visual check on the arrow's location and on the hand holding the laser beam was made by the experimenter throughout each trial. The experimenter's charge was to remind the participants of what their goal was if the arrow strayed out of the target region or if the hand moved. As in Balasubramaniam et al. (2000), the need to remind participants of the two task requirements never arose beyond the few practice trials used to acquaint the participants with the task.

Each participant was given 40 randomized trials, with the laser pointer held 20 times in each hand. In each set of 20 hand-designated trials, there were five trials at each level of task difficulty. Data collection began when the participants indicated that their stance was stable and they could maintain the arrow within the target region.

2.2. Results

Precision. Performance on the precision task itself was of secondary importance. Participants were requested only to keep the laser arrow within the boundaries of the white square defining the target. As in Balasubramaniam et al. (2000), the arrow's behavior beyond the preceding requirement was not at issue. In both the experiments of Balasubramaniam et al. (2000) and the present experiment, the sizes of the target regions were chosen such that, for each distance, once the laser arrow was positioned inside a target region, it was a simple enough matter for the participant to keep it there. Fluctuations of the arrow remained within the boundaries of a target region; they did not stray outside the boundaries once a trial began. In short, the precision task, as defined, was satisfied in all conditions by all 12 participants.

Root mean square (RMS) variability. Mean RMS variability over the five trials at each combination of target size and distance was computed for each participant. These mean RMS values for each participant as a function of direction of sway, handedness and the hand holding the laser pointer are summarized in Table 1. As expected, the fluctuations were very small, typical of COP motion during quiet standing. Across participants and experimental conditions, mean RMS variability ranged from 2.8 to 5 mm.

A particularly striking and important feature of Table 1 is the confirmation of the division by handedness: all six designated left-handed participants behaved oppositely to all six designated right-handed participants. For example, in respect to AP sway, inspection of Table 1 reveals that whereas left-handed participants uniformly exhibited less variability when the pointer was on the left side, right-handed participants exhibited less variability when the pointer was on the right side.

The data of Table 1 were analyzed by an Analysis of Variance (ANOVA) with a between subjects factor of handedness (2) and within subjects factors of side (2), difficulty (4) and sway direction (2).

Effect of task difficulty. As shown in Fig. 1, ML sway decreased, and AP sway increased with task difficulty. The interaction was significant: $F(3, 15) = 616.42$, $p < 0.0001$. There was also a main effect of task difficulty, $F(3, 15) = 32.87$, $p < 0.0001$.

Table 1
Mean RMS of AP and ML sway as a function of hand holding the laser pointer and task difficulty in Experiment 1

Subject	Left-hand								Right-hand							
	ID1		ID2		ID3		ID4		ID1		ID2		ID3		ID4	
	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML
Left-handers																
1	3.68	3.28	3.86	3.02	3.88	3.06	4.01	2.85	4.12	3.02	4.35	2.82	4.33	2.79	4.54	2.65
2	3.68	3.30	3.88	3.20	3.81	3.01	3.99	2.96	4.01	3.07	4.32	2.91	4.29	2.83	4.53	2.76
3	3.62	3.29	3.80	3.16	3.87	3.07	4.11	2.87	4.11	3.04	4.41	2.90	4.28	2.81	4.52	2.69
4	3.61	3.25	3.91	3.10	3.83	3.10	4.10	2.72	4.10	2.96	4.29	2.81	4.38	2.77	4.51	2.66
5	3.61	3.29	3.89	3.25	3.84	3.02	4.13	2.97	4.04	3.02	4.36	2.85	4.39	2.80	4.49	2.59
6	3.59	3.28	3.75	3.24	3.85	3.05	4.02	2.86	3.99	3.03	4.32	2.84	4.37	2.79	4.56	2.67
Right-handers																
1	4.31	3.36	4.52	3.23	4.72	3.17	4.91	3.00	3.32	3.55	3.81	3.40	3.82	3.32	3.93	3.21
2	4.23	3.37	4.55	3.28	4.71	3.18	5.01	3.04	3.30	3.49	3.79	3.39	3.80	3.33	3.91	3.28
3	4.34	3.38	4.49	3.26	4.73	3.16	4.95	2.98	3.35	3.47	3.79	3.38	3.79	3.36	3.98	3.25
4	4.32	3.36	4.56	3.30	4.81	3.11	4.88	3.02	3.31	3.52	3.70	3.35	3.88	3.39	3.90	3.19
5	4.26	3.38	4.51	3.29	4.84	3.12	4.97	3.04	3.32	3.58	3.54	3.37	3.81	3.34	3.87	3.22
6	4.40	3.37	4.62	3.29	4.70	3.16	5.02	3.01	3.31	3.53	3.53	3.39	3.85	3.35	3.92	3.24

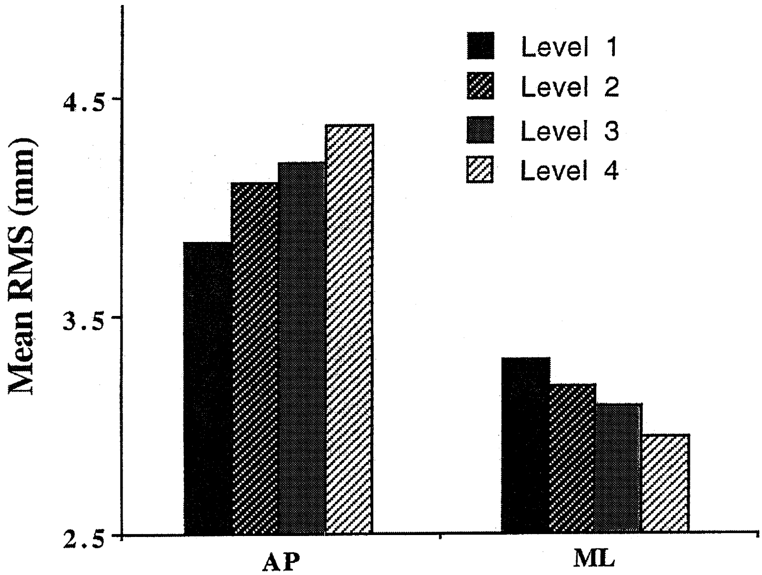

Fig. 1. The difficulty of the precision aiming task in Experiment 1 affected mean RMS variability in the ML and AP directions differently. Levels 1–4 stand for index of difficulty.

The observed decrease in RMS in the ML direction with level of task difficulty indicates that ML sway was reduced systematically in order to achieve the requisite precision of aiming. The corresponding observation of an increase in RMS of AP sway with level of difficulty suggests that, as the task demands became more severe, responsibility for maintaining postural balance was increasingly assumed by the subsystem governing AP fluctuations (Balasubramaniam et al., 2000).

Left–right contrast and RMS variability. Fig. 2 indicates that the effects on AP and ML sway of holding the laser pointer in the right or left hand depended on the handedness of the participant, $F(1, 5) = 2323.95$, $p < 0.0001$. AP fluctuations were less when the laser pointer was on the preferred side than when the laser pointer was on the non-preferred side. That is, right handers exhibited smaller AP fluctuations when holding the laser pointer in the right hand and left handers exhibited smaller AP fluctuations when holding the laser pointer in the left hand. The opposite was the case for the ML direction. When the laser pointer was on the non-preferred side, ML fluctuations were less than when the laser pointer was on the preferred side.

Handedness and RMS variability. Fig. 3 shows that right handers exhibited more variability than left handers. The ANOVA confirmed this difference:

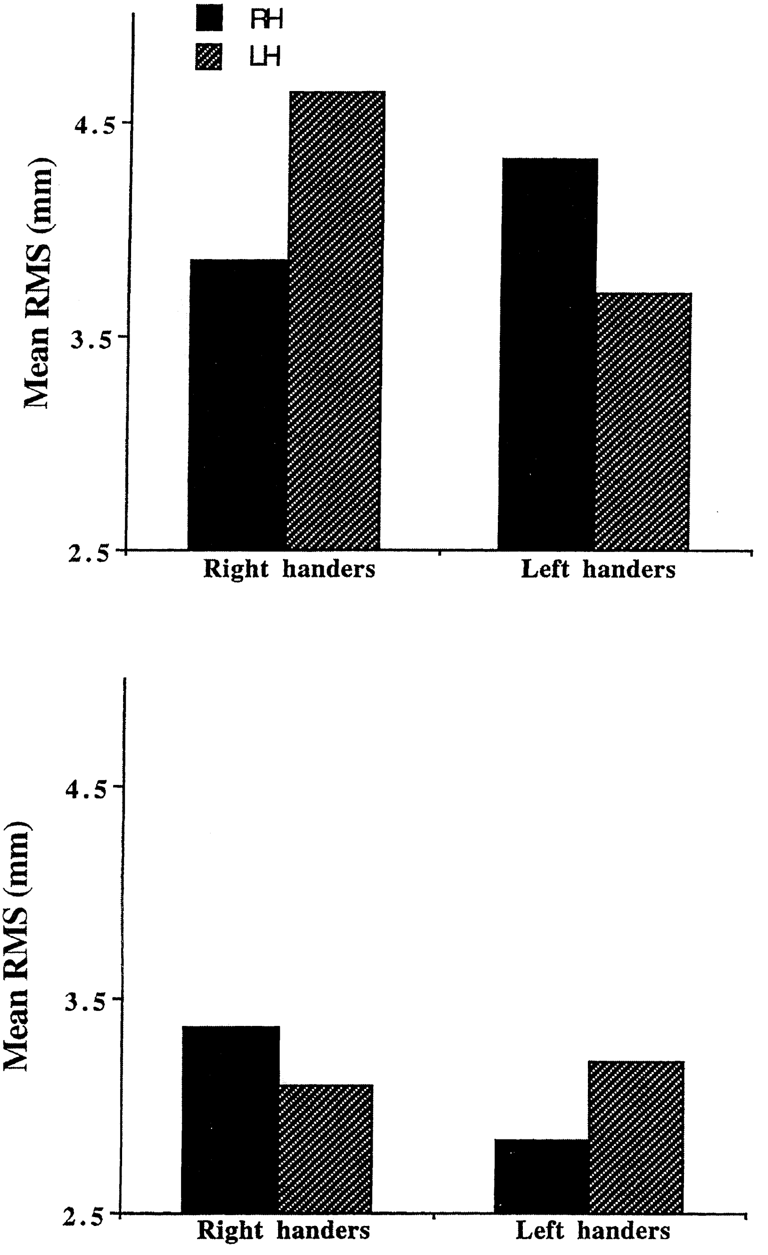

Fig. 2. The upper and lower panels show, for AP and ML sway, respectively, the interaction in Experiment 1 of handedness with the hand (RH = right-hand, LH = left-hand) holding the laser pointer.

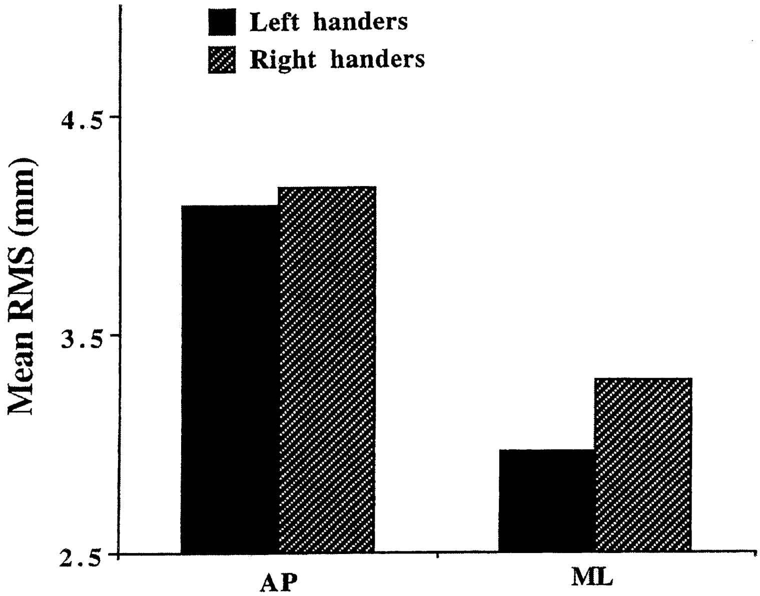

Fig. 3. Postural sway of right-handed participants in Experiment 1 was greater than that of left-handed participants.

$F(1, 5) = 1449.19$, $p < 0.001$. It also revealed that the magnitude of the contrast was greater in the ML direction than in the AP direction, $F(1, 5) = 253.62$, $p < 0.0001$. That is, regardless of which hand held the pointer, right-handed subjects were more variable in the position of COP than left-handed subjects.

2.3. Discussion

The present results may be interpreted as evidence favoring Geschwind and Galaburda's (1987) conjecture. Satisfying precision aiming in the present experiment, with the participant's coronal plane parallel to the target's plane, required a systematic reduction in ML fluctuations. Meeting this requirement proved to be dependent upon the participant's hand preference. The magnitude of variability in the ML direction decreased with target difficulty, in confirmation of the findings of Balasubramaniam et al. (2000), with the overall decrease greater when the pointer was on the non-preferred side rather than the preferred side. In comparison, AP fluctuations increased with target difficulty, with the overall increase greater when the pointer was on the preferred side rather than non-preferred side (Balasubramaniam et al., 2000).

The role of AP sway in the present experiment was primarily in respect to preserving upright posture rather than aiming. How should its increase relative to ML's corresponding decrease be understood? It has been hypothesized that a certain amount of variability is essential for standing (Schieppatti, Hugon, Grasso, Nardone & Galante, 1994). If variability in one direction of sway is restricted, for whatever reason, more variability must occur in the unrestricted direction. Parkinson's patients exhibit impaired movement in the AP direction possibly due to amplified ankle muscle stiffness. Their response to this reduction in AP sway is an elevated degree of ML sway (Mitchell, Collins, DeLuca, Burrow & Lipsitz, 1995), presumably to achieve the needed level of postural stabilizing activity in the face of the reduced contribution of AP activity. The present finding of augmented variability in the AP direction in the face of reduced variability in the ML direction may be similarly interpreted (see Balasubramaniam et al., 2000).

More resistant to explanation is the particular relative patterning of ML and AP sway induced by drawing attention to the preferred side (e.g., a right-handed person holding the pointer in the right hand). What mechanism is implied by a smaller decrease in ML variability and a larger increase in AP variability when attention was drawn to the preferred side compared to when it was drawn to the non-preferred side? Why the latter pattern rather than the reverse? If the AP sway in the present experiment is interpreted as compensatory, as suggested above, then the issue is that of why the subsystem producing ML sway was deactivated less by the demands of precision when attention was directed to the preferred side.

One possible resolution of the preceding issue follows from the notion that the laterality of postural control is realized, in part, as a subtle bias toward one hip rather than the other. The hip abductors and adductors are responsible for producing the loading of the limbs (by raising and lowering the body mass above the pelvis), that is, they are responsible for generating the vertical reaction forces under the feet (Winter, Prince, Stergiou, & Powell, 1993). It is this loading (and unloading) of the legs that characterizes the hip system's contribution to standing upright (Winter et al., 1996). For most people, the proposed hip bias would be to the hip on the same side as the manual preference – that is, the right hip for right-handers and the left hip for left-handers. More activity in the abductors and adductors of the preferred hip might produce more variable vertical force on the preferred side than on the non-preferred side. In performing the precision aiming task, the activity of the abductors and adductors of both hips must be reduced. If it is the case, however, that drawing attention to the preferred side magnifies the laterality of the hip system, then the possibility arises that the muscular activity of the preferred hip will be reduced less in response to precision demands when the pointer is on the preferred side. Experiments with a split force platform (Winter et al., 1996) would be needed to test this hypothesis. It is worth noting, perhaps, that other research on laterality, attention and performance has found similarly complex findings requiring a hypothesis much like ours. For example, Kinsbourne and Cook (1971) reported that balancing a dowel with the non-preferred hand was enhanced by concurrent speaking relative to silence. The same task performed by the preferred hand was performed less well in the concurrent speaking condition. Kinsbourne and Cook (1971) proposed that the enhanced left-hand performance arose because the concurrent task was just sufficient to distract attention from the balancing task but not demanding enough to absorb attention fully.

Clearly, resolution of the issues raised by the present handedness-dependent pattern of AP and ML fluctuations requires a more thorough understanding of postural dynamics and laterality's role than that available at the present time.

3. Experiment 2

The choice of the precision aiming task of Experiment 1 was motivated by the hypothesis that task asymmetry enhances the manifestation of the body's functional asymmetry (e.g., Amazeen et al., 1997; Peters, 1994). In Experiment 2 we examined the postural behaviors of left-handed participants and right-handed participants in the absence of imposed lateral biases in attention. We did not expect to find support for Geschwind and Galaburda's (1987) conjecture.

The participants of Experiment 2 simply stood and looked at the targets (which were of the same sizes and at the same distances as those of Experiment 1). Under conditions of binocular fixation on distal targets, experiments have shown that AP and ML sway exhibit similar behavior: both increase with the increasing distance and/or decreasing size of the fixated target (e.g., Paulus, Straube, Krafcyzk & Brandt, 1989). This outcome has been taken as evidence that visual stabilization of posture in the AP and ML directions depends on the efficiency with which oscillations of the body can be detected relative to stationary environmental surfaces. In the view of Paulus et al.

(1989), deterioration of visual stabilization with increasing distance or decreasing size of a fixated target arises because of the reduced magnitude of retinal displacement caused by head sway during fixation of the target.

Experiment 1 found two effects related to handedness. One effect was the interaction of sway direction and hand preference. The other effect was the smaller overall level of COP fluctuations for left-handers. Whereas the former effect seems to demand task asymmetry, the latter does not. An important question addressed by Experiment 2 was whether the mean difference in postural fluctuations due to handedness would persist under the conditions of Experiment 2.

3.1. Method

Subjects. Twelve undergraduate students from the University of Connecticut participated in this study. Six were self-proclaimed right-handers and six were self-proclaimed left-handers who satisfied the criteria of using the preferred side of the body for both throwing and kicking. Three of the right-handers and three of the left-handers were female. The ages of the participants ranged from 17 to 23 years, with a mean of 18.9 years. Their body weights ranged from 40 to 92 kg, with a mean of 59.6 kg. None of the participants reported any abnormalities or injuries at the time of the experiment. All participants had normal or corrected to normal vision

Apparatus, data collection and stimuli . The basic features of Experiment 2 replicated those of Experiment 1.

Procedure. Participants stood on the force platform in a well-lit room with all the surrounds visible. They stood with arms by the side and feet abducted 10°. The focal task on each trial was to fixate the target oriented in a plane parallel to the coronal plane of the body. Data collection for each trial began when the participants reported that the target was fixated. There were 40 randomized trials of 30 s duration each, 10 per each configuration of target distance and size. The interval between trials was dictated by the participants' comfort level. It ranged from 40 s to 1.5 min.

3.2. Results

RMS analysis. Mean RMS variability over the 10 trials at each combination of target size and distance was computed for each participant. These mean RMS values for each participant as a function of direction of sway are summarized in Table 2. Fig. 4 summarizes the overall RMS means as a

Table 2
Mean RMS of AP and ML sway as a function of task difficulty in Experiment 2

Subject	Left-handers								Right-handers							
	ID1		ID2		ID3		ID4		ID1		ID2		ID3		ID4	
	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML	AP	ML
1	3.85	3.59	3.91	3.57	4.12	4.45	4.17	4.13	3.97	3.63	4.26	4.18	4.43	4.32	4.49	4.42
2	4.03	4.18	4.25	4.21	4.39	4.27	4.52	4.49	4.15	4.08	4.21	4.10	4.22	4.13	4.27	4.29
3	3.78	3.82	3.88	3.84	3.99	4.13	4.02	3.98	3.98	3.46	4.03	4.02	4.17	4.16	4.32	4.30
4	3.78	3.85	3.83	3.83	3.90	3.99	4.13	4.08	4.02	3.99	4.13	4.08	4.20	4.22	4.23	4.28
5	3.62	3.65	3.65	3.66	3.80	3.78	3.86	3.88	3.57	3.57	3.70	3.69	3.99	3.94	3.91	3.92
6	4.18	4.12	4.25	4.22	4.33	4.22	4.43	4.50	4.16	4.15	4.22	4.28	4.29	4.33	4.35	4.27

function of handedness, sway direction and ID. The ANOVA revealed only a main effect of task difficulty, $F(3, 15) = 35.260$, $p < 0.0001$.

3.3. Discussion

Experiment 2 confirmed the previous demonstrations of Paulus et al. (1989): both directions of COP activity were associated with increasing variability as target size decreased and target distance increased. This effect has been interpreted as indicating that visual stabilization of posture in the AP and ML directions depends on how effectively the fluctuations of the body can be detected relative to stationary environmental surfaces. Notably, there were no effects of handedness. The functional asymmetry of the body did not manifest itself in steady-state postural fluctuations under the symmetric task conditions of Experiment 2.

4. General discussion

In sum, the results of Experiments 1 and 2, taken together, point to a lateralization of whole-body control that is made apparent when the task of standing still is incorporated in another task that biases attention to one side of the body rather than the other. The possibility that lateralization extends beyond fine manual tasks to coordination of trunk and limbs has been referred to in the present article as Geschwind and Galaburda's (1987) conjecture.

Although there are no previous specific tests of this conjecture to our knowledge, hints as to the appropriateness of the conjecture are to be found in the literature. Thus, Rode, Tiliket and Boisson (1997) reported that ML

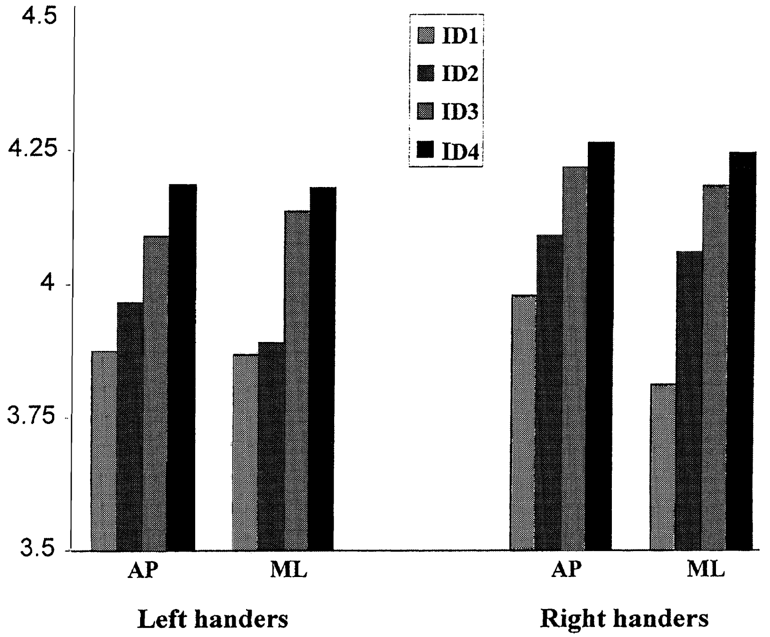

Fig. 4. Level of difficulty of the targets requiring visual focus in Experiment 2 affected mean RMS variability in the ML and AP directions in the same way.

sway of COP in hemiparetic patients was larger towards the side of the lesion than the corresponding sway of normals. Further, left hemiparetic patients showed greater ML sway compared to right hemiparetic patients.

As noted in the introduction, Geschwind and Galaburda had remarked on the possible elusiveness of an asymmetry in axial movements. They doubted that it would be readily detected in standard performance tests and questionnaires, for example. The challenge, therefore, is to find tasks that make the lateralization evident. In other movement domains, small lateralization effects present when both sides of the body – both upper limbs, for example – must produce the same rhythm, are made more evident under particular experimental conditions. They can be increased, for example, by increasing the speed of the movement (Treffner & Turvey, 1996) or by focusing attention on one side rather than the other (Amazeen et al., 1997; Riley et al., 1997). The present research reinforces the understanding that the laterality of ostensibly symmetric movements, such as those termed axial by Geschwind (1975), can be made manifest in the context of tasks that impose an asymmetry of attention and/or effort.

In the absence of such an imposed task asymmetry, Experiment 2 failed to detect any difference between left-handed and right-handed participants. Even the direction-independent handedness effect of Experiment 1 – a lower level of COP fluctuations in left-handed participants – was not replicated in Experiment 2. One should, of course, be circumspect about the reliability of the handedness main effect of Experiment 1. It may simply be a peculiarity of sampling (there were only six left-handers and six right-handers). If, however, it proves to be a true expression of laterality, then it could be of significance to understanding the nature of handedness. The neural bases for manual and axial movements are assumed to be different – primarily pyramidal and primarily non-pyramidal, respectively (e.g., Brodal, 1992; Geschwind, 1975). Perhaps a full account of handedness will require an appreciation of how functional asymmetry is manifest in both neural substrates.

We conclude with the question that motivated the research of Balasubramaniam et al. (2000): how is postural sway constrained in the performance of a precision aiming task, such as archery or rifle shooting? The goal of the preceding research was to understand how postural sway meets the dual challenges of precision aiming and standing upright and how the meeting of these challenges varies with the difficulty of the precision aiming task. The results of Balasubramaniam et al. (2000) suggested that a postural organization for upright standing and aiming entails two independent postural subsystems with different but reciprocally related dynamics. The results also suggested that some definite amount of postural variability is needed to ensure stability while aiming. The findings of the present research reinforce both of the preceding conclusions and suggest one other, namely, that the postural organization for upright standing and aiming is lateralized.

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