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Research report

Asymmetries in motor attention during a cued bimanual reaching task: Left and right handers compared

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ABSTRACT

Several studies have indicated that right handers have attention biased toward their right hand during bimanual coordination (Buckingham and Carey, 2009; Peters, 1981). To determine if this behavioral asymmetry was linked to cerebral lateralization, we examined this bias in left and right handers by combining a discontinuous double-step reaching task with a Posner-style hand cueing paradigm. Left and right handed participants received a tactile cue (valid on 80% of trials) prior to a bimanual reach to target pairs. Right handers took longer to inhibit their right hand and made more right hand errors, suggesting that their dominant hand was more readily primed to move than their non-dominant hand, likely due to the aforementioned attentional bias. Left handers, however, showed neither of these asymmetries, suggesting that they lack an equivalent dominant hand attentional bias. The findings are discussed in relation to recent unimanual handedness tasks in right and left handers, and the lateralization of systems for speech, language and motor attention.

1. Introduction

Manual laterality is a defining feature of our species, with approximately 90% of the population being right handed (Coren and Porac, 1977). Unfortunately, attempts to determine the underlying cause of manual asymmetries have met with mixed success (for a recent review, see Goble and Brown, 2008). One interesting, but under reported hypothesis suggests that subtle asymmetries are best elicited during bimanual tasks where attention is being divided between the hands. Peters (1981) suggests that this division of attention is asymmetrical, with the right hand of right handers receiving a larger 'share' of the attentional resource. He further suggests that this attentional bias may underlie the right hand advantage that the majority of the population exhibit in conventional unimanual tasks (Peters, 1995).

Peters (1981) reported that right handers found it very difficult to coordinate their limbs in a simple bimanual tapping task when the left hand was assigned a more attentionally-demanding task portion than the right hand. The crucial, asymmetry-inducing manipulation in this experiment was that the task required both hands to be moving at the same time – participants were perfectly capable of performing the easy or the difficult tasks with either hand equally well under unimanual conditions. The marked asymmetries appeared only when attention was divided by the concurrent

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use of both hands. Researchers have noted similar asymmetries using sophisticated rhythmic bimanual coordination paradigms. The initial demonstrations of small, but consistent attentional asymmetries during a rhythmic pendulum oscillation task by Treffner and Turvey (1995) have been advanced by experiments using a bimanual circling paradigm (e.g., Rogers et al., 1998) and a variety of imaginative attentional manipulations (e.g., Amazeen et al., 1997; De Poel et al., 2006). In contrast to the impressive variety of work examining attentional asymmetries during rhythmic tasks, very few studies however have provided any evidence of an attentional bias during *discrete* bimanual coordination (for a notable exception, see Honda, 1982).

In a recent study, we investigated attentional asymmetries during visually-guided bimanual reaches with a discontinuous double-step reaching task (Buckingham and Carey, 2009). In this task, a bimanual reach to a target pair was followed by a unimanual reach to a single target. This unimanual target appeared halfway through the bimanual portion of the reach, when attention was divided between the limbs. A clear pattern of asymmetries emerged from the participants: their right hand was quicker to react to this newly appearing target, in stark contrast to the standard pattern of reaction time asymmetries seen in unimanual reaching tasks (the *left hand* generally has the faster reaction time in right handers – see Carson, 1996 for review). This asymmetry in the downtime (the ‘refractory period’) between the bimanual and unimanual reach portions was taken as an indication of the direction of attention during the bimanual part of the task. This conclusion was supported by a follow-up experiment, where altering the direction of overt attention during the double-step task changed the magnitude and direction of the refractory period asymmetry correspondingly (i.e., the hand which was overtly attended showed a reduced refractory period). Thus, the rightward asymmetry demonstrated in the initial experiment was likely to have attentional underpinnings.

The nature of this bias in attention, however, remains underspecified. The bias that was demonstrated in the rhythmic tasks of Peters (1981), Amazeen et al. (1997) and others likely refers to a difference in the temporal monitoring of the hands. Yet, given that Honda (1982) noted that right handers tend to make rightward saccades during bimanual reaching, an attentional bias is also likely to occur at the visual or somatosensory levels (i.e., related to input). Any bias that occurs at the level of input may affect output-level mechanisms, given the feedback and feedforward demands of a goal-directed reach (for a review of these demands, and their possible control mechanisms, see Wolpert and Flanagan, 2001). Thus, it is probable that attentional asymmetries at input (Honda, 1982) are accompanied by asymmetries at the level of movement selection.

Attempts to experimentally measure selection of one particular movement over another have led to the development of paradigms investigating the construct of ‘motor attention’, often referred to as ‘intention’ (Andersen et al., 1997; Rushworth et al., 1998; Snyder et al., 2000). This output-level attention is similar to suggestions that Kimura and others have made regarding a left lateralized system important for praxis (e.g., Kimura and Archibald, 1974). Disorders such as apraxia, following damage to the left cerebral hemisphere, are thought to be a consequence of damage to this system. However, the nature of the attentional, cognitive, and sensorimotor deficits associated with this family of disorders remains markedly underspecified (Goldenberg, 2009; Ietswaart et al., 2006, 2001; Petreska et al., 2007).

In an imaginative series of experiments, Rushworth and colleagues have demonstrated a lateralization of the neural substrates underlying intentional processing. Deficits induced in neurologically intact subjects using repeated transcranial magnetic stimulation (rTMS – Rushworth et al., 2001), imaging work with positron emission tomography (PET – Rushworth et al., 2001), and data from brain injury patients (Rushworth et al., 1998) in tasks that require selecting one of four fingers to press a button, all indicate that the neural network underlying intention is lateralized to left parietal regions. It is possible that dextrals’ bias for choosing the right hand over the left is related to dominant hand advantages for movement selection, through privileged intra-hemisphere access to the left-lateralized intention system (Verfaellie and Heilman, 1990).

While previous studies have demonstrated that attention is biased toward the right hand in dextrals (e.g., Buckingham and Carey, 2009), the neural locus of this bias is unknown. It is likely that the attentional bias described by Peters (1981) shares a considerable overlap with left lateralized motor attention system described by Rushworth et al. (1998). Cueing tasks have been successfully utilized to distinguish between and manipulate the direction of attention at both the input (Posner, 1978) and output (Bestelmeyer and Carey, 2004) levels. In order to adapt our bimanual paradigm to examine asymmetries in motor attention, we altered the double-step pointing task described above to include a Posner-style cue. In this new task, a vibro-tactile cue indicated which hand would have to perform the unimanual portion of the reach. This cue, which was valid for 80% of the trials, indicated which hand would have to complete the unimanual portion of the task (i.e., which hand the unimanual target would appear nearest to), ‘priming’ it for selection. However, when the cue was invalid, participants had to inhibit the primed response and reach with the other, non-cued, limb. Asymmetries in the length of time that right and left handers take to inhibit their movements during these invalid trials should indicate which hand was more primed for selection during the bimanual portion of the task. This implicit measure of the direction of motor attention is analogous to the cue-cost measure seen in classic Posner attention tasks (Posner, 1978). Indeed, if the cueing bias is particularly strong on a given trial, participants may fail to inhibit an inappropriate reach altogether and begin moving with the incorrect hand. These errors provide a secondary measure of the strength of any bias.

Overall, it is likely that the dominant hand of right handers will be more readily primed and thus perform *more poorly* than the less-favored counterpart, given that the vast majority of right handers show a consistent direction and degree of lateralization for motoric tasks such as language output. Specifically, a simple prediction would be that their dominant hand will be primed for selection and thus more readily cued than its counterpart, even on invalid trials. As the inhibition of a movement presumably takes some effort (manifesting as a temporal cost), invalidly-cued trials would be expected to have a longer refractory period than validly-cued trials.

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Therefore, we predicted that during invalidly-cued trials where a movement is successfully inhibited, the left hand of right handers would show a longer refractory period than the right hand due to the increased ‘cost’ of inhibiting the (more readily cued) right hand. Furthermore, right handers are likely to make more errors with their right hand.

The predictions are less clear for left handers. Data from rhythmic bimanual tasks is inconsistent, with some researchers demonstrating no consistent attentional biases (De Poel et al., 2006), while others find attentional asymmetries that outstrip those of their dextral sample (Amazeen et al., 1997). Furthermore, numerous studies of language laterality assessed by the Wada test (e.g., Rasmussen and Milner, 1977) or aphasia (e.g., Goodglass and Quadfasel, 1954) have provided data that less than 40% of left handers have language lateralized to the hemisphere that controls their dominant hand (cf. the ~90% value in dextrals). Thus, left handers appear to fall into distinct categories for speech and motor lateralization – typical (right hemisphere speech, right hemisphere motor dominance) and mixed (left hemisphere speech, right hemisphere motor dominance). If left lateralization for language functions is related to an attentional bias (Peters, 1995), as it is thought to be for other behavioral asymmetries (Goodale, 1990), then a substantial portion of a left handed sample will show larger effects of invalid cueing on their right, non-dominant hand. We predicted that the patterns of asymmetries that left handers show in this task will allow them to be grouped based on their individual patterns of lateralization for the praxis and language systems. Thus, while right handers should show clear difficulties with inhibiting their right hands during this task, only a relatively small proportion of the left handers should show equivalent left hand deficits, with the remaining adextrals perhaps showing similar right hand difficulties to the right handed sample.

2. Method

2.1. *Participants*

Thirty-five volunteers from the University of Aberdeen were recruited to take part in this experiment. The datasets from four participants were removed prior to analysis due to problems with the kinematic data collection, leaving a sample of 31 participants. Seventeen participants (3 males) were right-handed, as measured by a shortened version of the Waterloo Handedness Questionnaire (WHQ) (Steenhuis and Bryden, 1989; mean score = 25.8/30, SD = .9; mean age = 21.4 years, SD = 1.3), and 14 participants (7 males) were left handed (mean WHQ score = −19.3/30, SD = 10.6; mean age = 32.9 years, SD = 10.7). All participants had normal or corrected to normal vision and were naïve to the experimental hypotheses. Participants gave informed consent prior to testing, and all procedures were approved by the Ethics Committee of the School of Psychology at the University of Aberdeen.

2.2. *Apparatus and data reduction*

A horizontal light emitting diode (LED) grid and custom-written PC software were used to deliver the green central fixation (7.5 cd/m^2) and red target stimuli (6.5 cd/m^2). Small infrared reflective markers were attached to the left and right index fingers of each participant. The positions of these markers were monitored with a three-camera ProReflex motion analysis system (Qualisys inc.), recording at 240 Hz. The camera positions were calibrated in 3-dimensions prior to each testing session to ensure consistent spatial accuracy (<1 mm^3). The extracted text files, containing the relative position in X, Y and Z planes for each recorded frame of both markers, were digitally filtered with a dual pass 10 Hz Butterworth filter. The filtered data were then differentiated to yield velocity vectors which were combined to give the resultant velocities of each hand, using custom software written in Labview (National Instruments). From the resulting 3-dimensional velocity profile the onset and offset time *of each movement portion* for each hand was recorded. To account for residual forward motion between reach portions (see Buckingham and Carey, 2009), the movement onset and offset threshold was set at the relatively high value of 120 mm/sec. The refractory period measure was then calculated as the period between the offset of the bimanual portion of the reach and the onset of the unimanual portion of the reach (i.e., the period when the hand performing the double-step was moving slower than 120 mm/sec).

Small, custom built plastic cylinders (20 mm long and 13 mm in diameter) containing a 4 mm motor that rotated a small eccentric weight on its shaft at 180 Hz (1 mm amplitude) were attached to the top of each participant’s index fingers to deliver the vibration. These vibro-tactile stimulators were attached to the top surface of each participant’s index fingers with a Velcro strap. Prior to the start of each testing session, small test vibrations delivered concurrently to the participant’s fingers to ensure that the vibrations were readily detectable and felt roughly equivalent strength on both hands. Additionally, the vibro-tactile stimulators were swapped between the hands halfway through the experiment and the hand that each vibro-tactile stimulator started on was also varied between-subject (as is done with headphones in dichotic listening experiments – Bradshaw, 1990).

2.3. *Procedure*

Participants sat in front of the LED board on a height-adjustable chair with their fingers on home locations 18 cm apart, and performed a series of cued discontinuous double-step reaching movements. Prior to target onset, a fixation light appeared for a random duration between 700 and 1000 msec. This fixation light was extinguished at the same time as the onset of a target pair (with two possible positions). Participants were instructed to reach out and contact these targets as quickly and as accurately as possible with both hands simultaneously. Contacting these target pairs required a bimanual reach that was symmetrical about the midline of the participant, with an amplitude of between 19 and 22 cm (Fig. 1). Four hundred milliseconds after the appearance of this target pair (approximately halfway through the bimanual portion of the reach), a further single target appeared at a more distal location (20–22 cm). Participants were told to reach to this target with whichever hand was closest, *after* contacting the initial target pair.

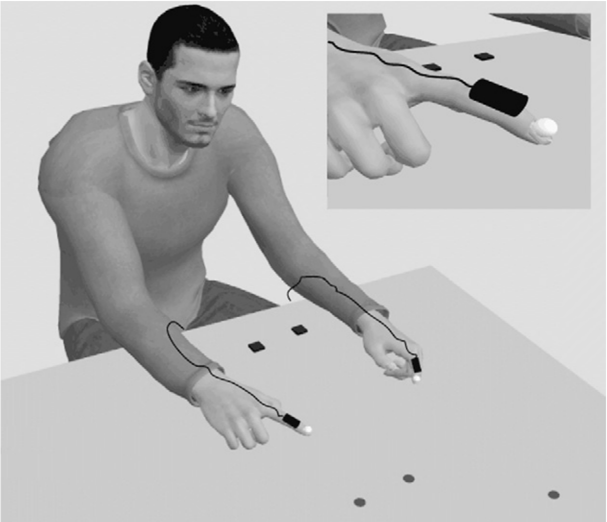

Fig. 1 – Detail of the positioning of the experimental setup (vibro-tactile stimulators and kinematic recording markers) and target layout during a trial. The unimanual target appeared approximately halfway through the bimanual portion of the double-step reach. Adapted from Buckingham et al. (2010).

At the same time as the initial target pair appeared, a vibration lasting 200 msec was delivered to one of the hands, serving as a cue to the participant that they would have to make the upcoming unimanual reach with that limb. This cue was 80% accurate (participants were told that the cue would provide an indication of the appropriate response hand most of the time, but would occasionally vibrate on the wrong hand). Therefore, (a) the hand vibrated, (b) the side of space where the eventual unimanual target would appear and (c) the hand required for the unimanual reach were always congruent in the validly-cued trials. For example, a right hand vibration would precede the appearance of a target in the right side of space, which would require a right hand movement (see Fig. 2a). However, in the invalidly-cued trials, the hand vibrated was *not* congruent with the side of space on which the target eventually appeared (and thus, the responding hand). These trials therefore required participants to resist making the pre-selected reach with the cued hand (i.e., to avoid reaching across the body) and to instead move their other, uncued, hand. In this case, a right hand vibration would precede the appearance of a target in the left side of space, requiring the participant to make a left hand movement (see Fig. 2b).

Upon completion of the double-step task, participants were told to maintain their landing positions until being asked to return to the home positions in preparation for the next trial. In total, participants undertook 200 double-step reaches, consisting of 20 invalidly- and 80 validly-cued trials per hand (all of which were randomly ordered), in a single testing session lasting 1 h.

2.4. *Analysis*

Only the trials where the final target appeared *during* the bimanual portion of the reach were included in the analysis. Therefore, all trials where the onset time of the bimanual portion of the double-step exceeded 400 msec (i.e., by the time the unimanual target had appeared) were removed. Additionally, all trials where the bimanual movement was completed before 400 msec had elapsed were also removed. Finally, all reaches with an initial bimanual onset of less than 150 msec were removed as anticipatory. These combined measures resulted in less than a 5% of trials being excluded.

In addition, trials where no refractory period could be measured (where, due to residual forward motion, participants failed to slow to the required movement offset trigger of 120 mm/sec during contact with the table) were removed. This problem affected only the validly-cued trials – interestingly, only in the right hand of five right handed participants. Consequently, a much higher proportion of validly-cued trials were removed than invalidly-cued trials (no more than 50% per individual however, independent of the trials excluded above). These losses of data are considered acceptable given the far higher proportion of validly-cued trials utilized in the cueing methodology – the vast majority of the trials removed were already in excess of the other condition. To clarify, the median value which was included in the inferential statistics was never taken from a condition with less than 40 trials in the validly-cued condition.

Trials where an *incorrect* hand movement was detected (by breaking the 3d-velocity threshold of 120 mm/sec) were recorded as error trials for that limb. On some of these error trials, the 'correct' hand did eventually move. However, as this eventual movement may have had resources depleted by the incongruous movement of the other (incorrect) hand, the refractory period scores for the error trials were removed prior to inferential statistical analysis. In other words, the refractory period scores on the invalidly-cued trials were numerically independent of any asymmetries that may have occurred as a result of different numbers of error trials in each hand.

The median refractory period times for each hand were calculated for the valid and invalid conditions. From these scores, a 'cue cost' was determined for each hand by subtracting the valid refractory period from the invalid refractory period. To test for the predicted asymmetries in cue cost, we performed a mixed design 2×2 analysis of variance (ANOVA) with hand (left/right) as the within-subject factor and handedness (left/right) as the between-subject factor. The ANOVA was followed by paired-sample *t*-tests to compare the cue cost for each hand, in addition to the mean number of errors made by each hand (on the invalidly-cued trials) across the different handedness groups. The coefficient of determination (r^2) is reported to indicate the proportion of the variance shared by the variables.

3. Results

Although left handers and right handers showed nearly identical overall cue-cost values (18.4 msec *vs* 17.3 msec respectively), the sample as a whole showed a higher cost of cueing for movements made with their left hand than their right hand (23.3 msec *vs* 12.4 msec; $F_{(1,29)} = 5.47$, $p < .05$). However, this main effect was not accompanied by an

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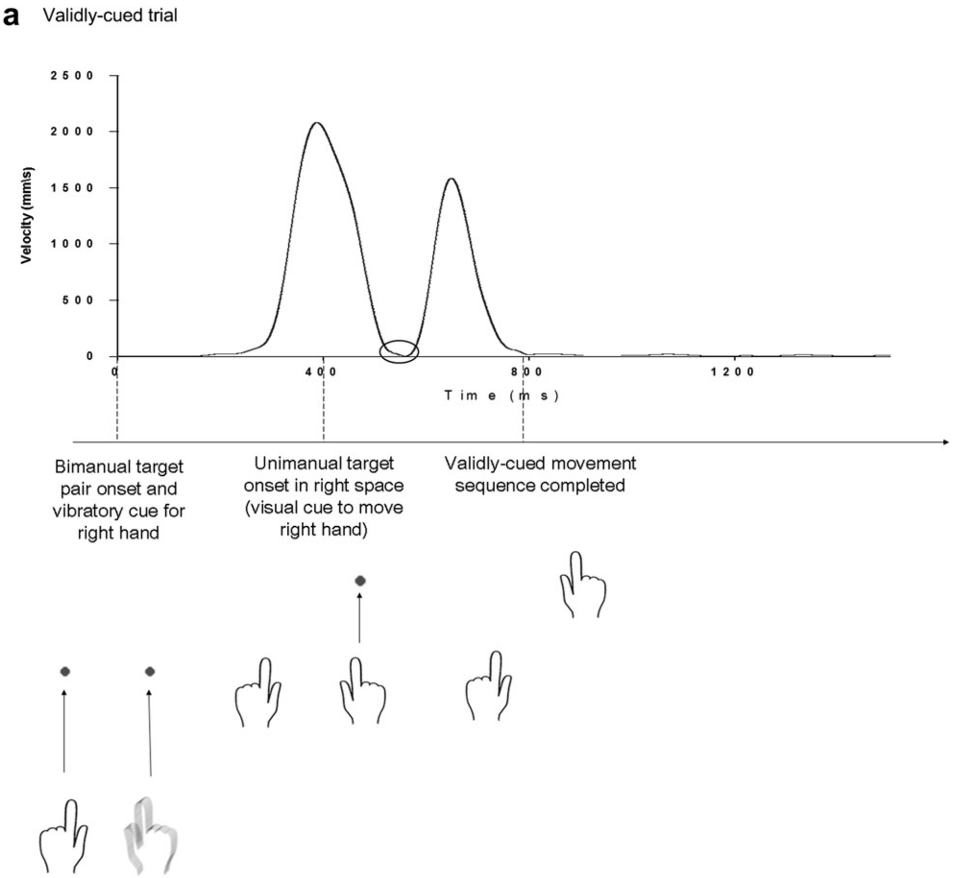

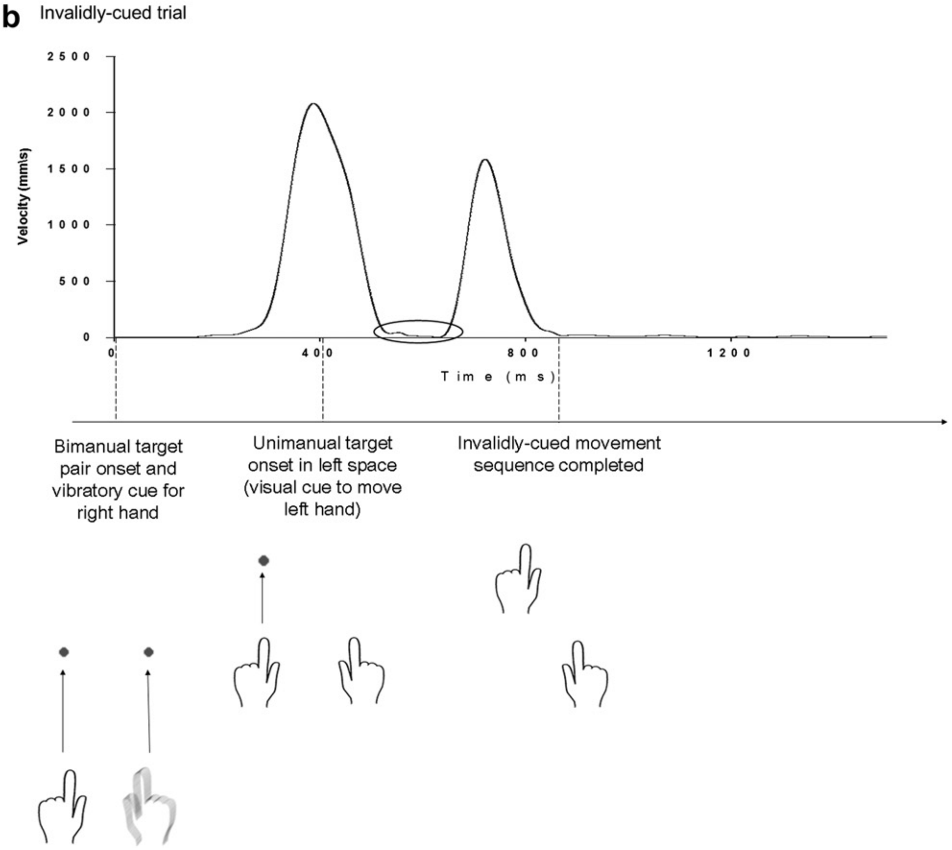

Fig. 2 – Examples of the (a) validly- and (b) invalidly-cued discontinuous double-step reaches. In the validly-cued trials, participants receive a vibration on the hand which must perform the second (i.e., unimanual) portion of the double-step reach. In the invalidly-cued trials, participants must inhibit the cued right hand response, and instead reach with their left hand (signalled by the leftward location of the visual target). Note the shorter downtime ('refractory period' – shown by an elipse) between the bimanual and unimanual reach portions during validly-cued trials. Adapted from Buckingham and Carey (2009).

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interaction between hand and handedness, which just failed to reach conventional levels of statistical significance ($F_{(1,29)} = 3.80$, $p = .06$). Given the comparatively small sample of each handedness group in relation to our previous work on attentional asymmetries (e.g., Buckingham and Carey, 2009), it is possible that the lack of interaction may have merely reflected a lack of power. Thus, rather than accepting the null hypothesis, we opted to examine the possibility of an interaction in greater detail. Planned comparisons showed that the right handers had a higher refractory period cue cost for their left hand than their right hand (28.4 msec *vs* 8.4 msec; $t(16) = 3.09$, $p < .005$, $r^2 = .137$; Fig. 3a), due to the lengthier durations associated with successfully inhibiting their left hands. Furthermore, right handers made more errors with their right hand than with their left hand (4.65 *vs* 2.71; $t(16) = 2.8$, $p < .05$, $r^2 = .108$; Fig. 3b). These results are both in the direction predicted by the hypothesis. Thus, right handers had more difficulty inhibiting their dominant hand, resulting in a longer refractory period for the non-dominant limb in successful trials and more errors with the dominant limb during unsuccessful trials.

In left handers however, there was no reliable difference between the right and left hands in terms of cue cost (18.3 msec *vs* 16.4 msec; $p > .7$; Fig. 3a) or errors (5.64 *vs* 4.50; $p > .2$; Fig. 3b). It would appear that, as a group, left handers found it equally challenging to inhibit either of their hands. There was no evidence of the left handed sample partitioning into 'sub-groups' with a right hand advantage or left hand advantage (Fig. 4). Rather, it appears that the left handers' pattern of data tended to group more closely around the diagonal than the right handers' data, indicating a lack of attentional asymmetries. Absolute refractory period values for the left and right handed samples are presented in Table 1.

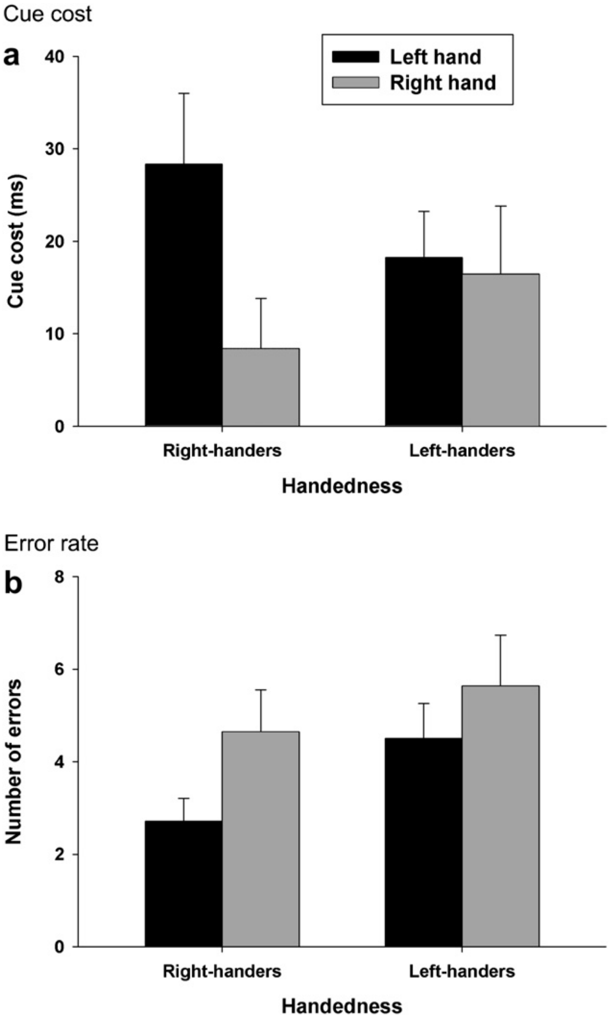

Fig. 3 – Comparisons between the hands in terms of (a) cost of cueing (validly-cued refractory period subtracted from the invalidly-cued refractory period) and (b) error rates, for left and right handers. The black and grey bars show the moving, rather than the cued hand.

4. Discussion

The current study examined whether right and left handed individuals have motor attention biased toward their dominant hand. The direction of motor attention during a bimanual reach was determined by examining how difficult it was to inhibit the cued movement of either hand – a measure of how over-prepared participants were to move their dominant or non-dominant hand following a period of attentionally-dividing bimanual coordination. The cued double-step reaching task yielded two related (but not confounded) measures to compare performance between the hands. The errors that participants made with either hand during invalidly-cued trials provided a direct indication of how difficult it was to inhibit that hand (i.e., inhibition failures), and, while the time taken (i.e., the cognitive resource, or effort) for participants to successfully inhibit an invalidly-cued movement was determined by the duration of the refractory period of the hand which eventually went on to complete the reach.

The results were unambiguous for the right handed sample. The right hand of right handers was pre-potentiated to make the follow-on unimanual reach in the current task, with the dextral sample showing a higher number of right hand errors, and a higher cue cost for their left hand. Therefore, building on previous findings (Amazeen et al., 1997; Buckingham and Carey, 2009), right handers appear to have attention for selection biased toward their right hand, priming it move. This attentional bias could conceivably be a major developmental factor in determining manual laterality in later life, as a consistent rightward bias would likely lead to a bias in the selection of the right hand for the more complicated portion of a bimanual task (Peters, 1995). Greater practice at complex tasks with the dominant hand would invariably lead to the performance differences between the limbs that characterize the asymmetries evident when right handers undertake more conventional unimanual tasks.

For the left handed sample however, there was no consistent pattern of asymmetries. For some, this difference between the left and right handed groups may be surprising, given that the majority of both handedness groups have language lateralized to the same cerebral hemisphere (Rasmussen and Milner, 1977). If language lateralization was a perfect predictor of

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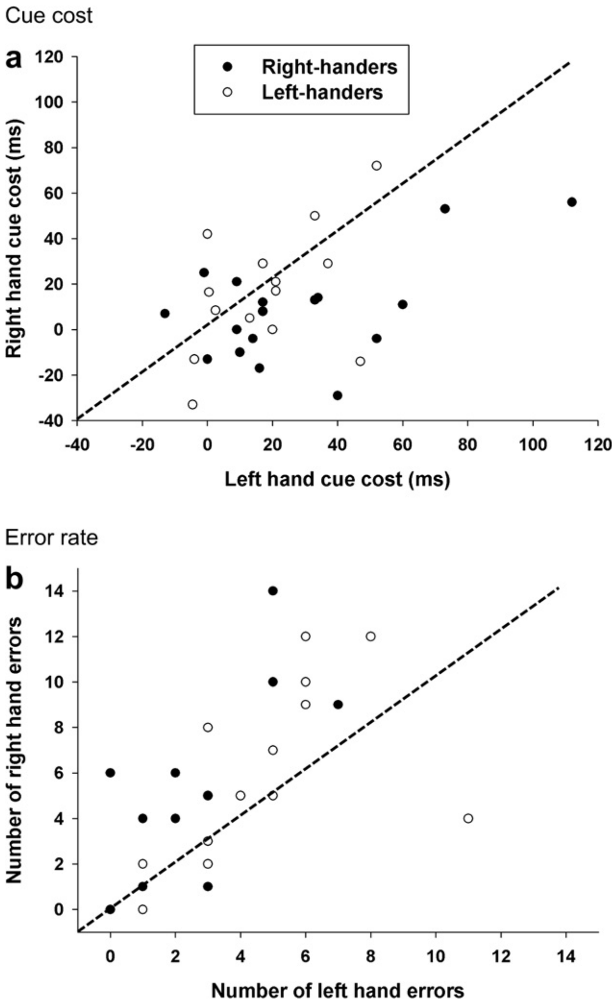

Fig. 4 – Scatter plots highlighting each left and right handed individual's degree of difficulty in inhibiting the left and right hands in terms of (a) cost of cueing and (b) error rates. Points above the diagonal indicate that an individual had a greater right hand cue cost or higher number of right hand errors, while points below the diagonal indicate the opposite.

attentional bias (or vice versa), then both groups would be expected to have similar behavioral profiles in the current task, albeit somewhat attenuated in the left handed group. Nevertheless, as left handers generally exhibit more bilateral and right hemispheric language lateralization on an individual level, we hypothesized that the left handed sample would divide into sub-groups based upon supposed cerebral laterality, which would have made the asymmetry a promising candidate for a behavioral marker in identifying atypical speech/motor lateralization. Yet, adextrals looked no more heterogeneous as a group than the right handed sample – the scatter of their data in Fig. 4 was merely shifted more toward the centre-spanning dotted line. The lack of asymmetries in the left handed participants indicated that they were equally proficient (although see the point below) at inhibiting invalidly-cued movements of the left or right hand (Fig. 3). This result may be related to the suggestion that left handers, at an individual level, are often more variable than right handers in many measures of performance (Goodale, 1990). Thus, rather than detecting adextral group-level variability, our measure appears to have tapped into left handed participants' individual variability – a factor that may be related to their apparent lack of attentional bias. It is interesting to note that these findings parallel the conclusions reached in a recent study by Gonzalez et al. (2007). In their hemispatial precision grasping task, they noted that left handers selected their non-dominant hand about 50% of the time, implying that network for controlling such actions is lateralized to the left hemisphere in both left and right handers.

It appears, to date, that our cued double-step task (and with it, biases in motor attention) may not prove to be a useful marker for predicting likely cerebral lateralization for some of the reasons discussed above. Other tasks might be more appropriate, such as gesturing during speech (cf. Kimura, 1973a, 1973b). Kimura (1993) also makes an intriguing suggestion that manual and oral praxis may be dissociable in left handers. If this proposition is correct, then manual behaviors of any sort are likely to be limited in their usefulness for predicting cerebral asymmetries, especially in adextral individuals. In spite of this caveat, our paradigm appears to be a useful tool for quantifying the degree of behavioral, and perhaps attentional, asymmetry at an individual level.

There is a further aspect of the comparison between left and right handers that warrants further discussion. While that the left handers' appeared to lack the asymmetry that was characteristic of the dextral portion of the sample, it is not certain whether this behavioral profile is advantageous or disadvantageous. Put another way, it is not clear whether left handers equally skilled at inhibiting movements with both hands, or equally poor. Although they did not receive direct statistical examination, the absolute refractory period scores (Table 1) may provide some insight into this puzzle. During invalidly-cued trials, neither of the limbs of the left handed portion of the sample

Table 1 – Absolute refractory period values for both hands of both handedness groups in the valid and invalid cue conditions (N.B., inferential statistics were performed on the difference scores, or cue-cost values only).

	Left handed participants		Right handed participants	
	Left hand refractory period (msec)	Right hand refractory period (msec)	Left hand refractory period (msec)	Right hand refractory period (msec)
Valid cue	78	72	61	48
Invalid cue	98	91	100	73

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managed to achieve a refractory period close to the dominant limb in right handers. Furthermore, left handers validly-cued refractory periods for either hand appeared to be longer than the refractory period seen in either of the right handers' limbs. Thus, as left handers appeared to be overall slightly worse at the task, it can be tentatively suggested that the left handed sample was equally poor at inhibiting either hand. This assertion is further supported by the overall error rate data, as left handers had more errors on average (5.1) compared to the right handed portion of the sample (3.7). What remains unclear, however, is whether there is something advantageous about asymmetries per se, or whether the apparent advantage in inhibition is directly related to dextrality.

The current study – the first to our knowledge to examine attentional asymmetries in right and left handers during discrete bimanual coordination, demonstrated different patterns for participants of different handedness. Dextrals had clear problems inhibiting their dominant hand, thus in this case were a victim to their rightward attentional biases. Adextrals however, showed no such asymmetry. Further research is required to make stronger claims about the developmental and evolutionary advantages of this attentional bias (or lack thereof).

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REFERENCES

Amazeen EL, Amazeen PG, Treffner PJ, and Turvey MT. Attention and handedness in bimanual coordination dynamics. *Journal of Experimental Psychology: Human Perception and Performance*, 23: 1552–1560, 1997.

Andersen RA, Snyder LH, Bradley DC, and Xing J. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, 20: 303–330, 1997.

Bestelmeyer PEG and Carey DP. Processing biases towards the preferred hand: Valid and invalid cueing of left versus right hand movements. *Neuropsychologia*, 42: 1162–1167, 2004.

Buckingham G and Carey DP. Rightward biases during bimanual reaching. *Experimental Brain Research*, 194: 197–206, 2009.

Buckingham G, Binsted G, Colino FL, deGrosbois J, and Carey DP. Gating of vibrotactile detetction during visually-guided bimanual reaches. *Experimental Brain Research*, 2010; doi:10.1007/s00221-009-2050-8.

Bradshaw JL. Methods for studying human laterality. In Boulton AA, Baker GB, and Hiscock M (Eds), *Neuromethods 17: Neuropsychology*. Clifton, UK: Humana Press, 1990: 225–280.

Carson RG. Putative right hemisphere contributions to the preparation of reaching and aiming movements. In Elliott D and Roy EA (Eds), *Manual Asymmetries in Motor Performance*. NY: CRC Press, 1996: 159–172.

Coren S and Porac C. Fifty centuries of right-handedness: The historical record. *Science*, 198: 631–632, 1977.

De Poel H, Peper CE, and Beek PJ. Handedness-related asymmetry in coupling strength in bimanual coordination: Furthering theory and evidence. *Acta Psychologica*, 124: 209–237, 2006.

Goble DJ and Brown SH. The biological and behavioural basis of upper limb asymmetries in sensorimotor performance. *Neuroscience and Biobehavioural Reviews*, 32: 598–610, 2008.

Goldenberg G. Apraxia and the parietal lobes. *Neuropsychologia*, 47: 1449–1459, 2009.

Gonzalez CLR, Whitwell RL, Morrissey B, Ganel T, and Goodale MA. Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, 182: 275–279, 2007.

Goodale MA. Brain asymmetries in the control of reaching. In Goodale M (Ed), *Vision and Action: the Control of Grasping*. Norwood, NJ: Ablex Publishing, 1990: 14–32.

Goodglass H and Quadfasel FA. Language laterality in left-handed aphasics. *Brain*, 77: 521–548, 1954.

Honda H. Rightward superiority of eye movements in a bimanual aiming task. *Quarterly Journal of Experimental Psychology*, 34A: 499–513, 1982.

Ietswaart M, Carey DP, and Della Sala S. Tapping, reaching and grasping in ideomotor apraxia. *Neuropsychologia*, 44: 1175–1184, 2006.

Ietswaart M, Carey DP, Della Sala S, and Dijkhuizen RS. Memory-driven movements in limb apraxia: Is there evidence for impaired communication between the dorsal and ventral streams? *Neuropsychologia*, 39: 950–961, 2001.

Kimura D. Manual activity during speaking-right-handers. *Neuropsychologia*, 11: 45–50, 1973a.

Kimura D. Manual activity during speaking-left-handers. *Neuropsychologia*, 11: 51–55, 1973b.

Kimura D and Archibald Y. Motor functions of the left hemisphere. *Brain*, 97: 337–350, 1974.

Kimura D. Adextrality. In *Neuromotor Mechanisms of Human Communication*. Oxford: Oxford University Press, 1993.

Peters M. Attentional asymmetries during concurrent bimanual performance. *Quarterly Journal of Experimental Psychology*, 33A: 95–103, 1981.

Peters M. Handedness and it's relation to other indices of cerebral laterality. In Davidson R and Hugdahl K (Eds), *Brain Asymmetry*. Cambridge, MA: MIT Press, 1995: 183–214.

Petreska B, Adriani M, Blanke M, Aude G, and Billard C. Apraxia: a review. In von Hofsten C and Rosander K (Eds), *Progress in Brain Research*, vol. 164. Elsevier, 2007: 61–83.

Posner MI. *Chronometric Explorations of Mind*. Hillsdale, NJ: Erlbaum, 1978.

Rasmussen T and Milner B. The role of early left-brain injury in determining lateralization of cerebral speech functions. *Annals of the New York Academy of Sciences*, 299: 255–269, 1977.

Rogers MA, Bradshaw JL, Cunnington RC, and Phillips JG. Inter-limb coupling in coordinated bimanual movement: Attention and asymmetries. *Laterality*, 3: 53–75, 1998.

Rushworth MFS, Ellison A, and Walsh V. Complementary localization and lateralization of orienting and motor attention. *Nature Neuroscience*, 4: 656–661, 2001.

Rushworth MFS, Nixon PD, Wade DT, Renowden S, and Passingham RE. The left hemisphere and the selection of learned actions. *Neuropsychologia*, 36: 11–24, 1998.

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Steenhuis RE and Bryden MP. Different dimensions of hand preference that relate to skilled and unskilled activities. *Cortex*, 25: 289–304, 1989.

Snyder LH, Batista AP, and Andersen RA. Intention-related activity in the posterior parietal cortex: A review. *Vision Research*, 40: 1433–1441, 2000.

Treffner P and Turvey MT. Handedness and the asymmetric dynamics of bimanual rhythmic coordination. *Journal of Experimental Psychology: Human Perception and Performance*, 19: 318–333, 1995.

Verfaellie M and Heilman KM. Hemispheric asymmetries in attentional control: Implications for hand preference in sensorimotor tasks. *Brain and Cognition*, 14: 70–80, 1990.

Wolpert DM and Flanagan JR. Motor prediction. *Current Biology*, 11: R729–732, 2001.

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