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ABSTRACT

Much debate in the handedness literature has centred on the relative merits of questionnaire-based measures assessing hand preference versus simple movement tasks such as peg moving or finger tapping, assessing hand performance. A third paradigm has grown in popularity, which assesses *choices* by participants when either hand could be used to execute movements. These newer measures may be useful in predicting possible “reversed” asymmetries in proportions of non-right handed (“adextral”) people. In the current studies we examine hand choice in large samples of dextral (right handed) and adextral participants. Unlike in some previous experiments on choice, we found that left handers were as biased towards their dominant hand as were right handers, for grasping during a puzzle-making task (study 1). In a second study, participants had to point to either of two suddenly appearing targets with one hand or the other. In study 2, left handers were not significantly less one handed than their right-handed counterparts as in study 1. In a final study, we used random effects meta analysis to summarise the p**o**ssible differences in hand choice between left handers and right handers across all hand choice studies published to date. The meta analysis suggests that right handers use their dominant hand 12.5% more than left handers favour their dominant hand (with 95% confidence that the real difference lies between 7 and 18%). These last results suggests that our two experiments reported here may represent statistical Type 2 errors. This mean difference may be related to greater left hemispheric language and praxic laterality in right handers. Nevertheless, more data are needed regarding the precise proportions of left and right handers who favour their preferred hands for different tasks.

INTRODUCTION 1.0. One hand or the other? Effector selection biases in right and left handers.

Right hand preferences for skilled activities such as handwriting and throwing are typically associated with left hemispheric specialisation for speech and language (Knecht, Drager, Deppe, Bobe, Lohmann, Floel et al., 2000; McManus, 2002; Rasmussen & Milner, 1977; Van der Hagen, Cai & Brysbaert, 2012). This relationship implies that the articulatory requirements of speaking may be a crucial component of the left hemispheric system and may confer some advantages to the limbs controlled by the same hemisphere (Carey et al., 2009; Goodale, 1988; Kimura, 1993; Rushworth, Ellison, & Walsh, 2001; Rushworth, Johansen-Berg, Göbel & Devlin, 2003; Rushworth, Krams, & Passingham, 2001). Evidence for this idea has been obtained from the study of patients with manual apraxia, a disorder which involves poor production of movements to command (and or copying movements) in spite of relatively intact strength and position sense (Goldenberg, 2013). Apraxic patients predominantly have lesions in the left hemisphere, yet (when they are testable) both of the hands often display approximately equal levels of difficulty with movement imitation (Kimura, 1993; Kimura & Archibald, 1974). In fact, aphasic patients are often apraxic, and even when the deficits occur in isolation, problems with non-speech oral movements can be found. Selection of appropriate movements and planning how these movements will be joined together in a sequence have been of particular relevance (Kimura, 1982).

In spite of early assumptions of right hemispheric dominance for speech and language in left-handed people (Harris, 1991), it is now well established that approximately 70% of any large sample of left handers will actually be more reliant on the left hemisphere for speech and language (e.g. Knecht et al., 2000; see Carey & Johnstone, 2014, for review). Therefore, if the praxic system overlaps with speech lateralisation (at least in terms of being in the same hemisphere), then a substantial proportion of any sample of left handers will have the praxic system in the hemisphere which controls their *non-dominant hand*. In such cases, the non-dominant hand might be subtly advantaged, and/or the dominant hand subtly disadvantaged, compared to the dominant and non-dominant hand of the right hander.

In tasks such as visually-guided aiming, in right handers, the right hand is superior to the left in terms of speed and accuracy (Carnahan, 1998; Fisk & Goodale,

1985) although reaction times of the left hand can be lower than those of the right (Boulinguez, Barthélémy, & Debu, 2000; Carson, Chua, Goodman, Byblow, & Elliot, 1995). In contrast, left handers tend to be slower to initiate a movement and reach a lower peak velocity than their right-handed counterparts (Goodale, 1990). More crucially, as a group they were relatively symmetrical compared to the right handers. In other words, left handers are less lateralised than right handers, as one hand was not greatly superior to the other. According to Goodale (1990), the "odd hand out" is the right hand of the right hander, which in the vast majority of any such sample will have "privileged access" to the sensorimotor control systems of the speech–dominant left hemisphere. However, in other experiments, some data suggest that left handers as a group behave like right handers (literally. e.g. right hand duration and accuracy advantages, left hand reaction time advantages) in terms of right and left hand kinematics, supporting a link between hand movement asymmetries and probable speech lateralisation (Boulinguez, Velay, & Nougier, 2001). Clearly, sampling error can be an issue with left handers, unsurprisingly.

Kinematic studies such as these require expensive equipment and extensive off-line data analysis, which partially explains why, unfortunately, the sample sizes tend to be somewhat limited. Studies of hand *choice,* on the other hand*,* rather than hand kinematics might be advantageous for larg**er-**sample testing. Once the within-participant reliability of any measure has been established (which could allow for relatively short testing sessions if the effects are robust), they can be administered to large samples with only the requirement of accurate recording of choice by an experimenter. In fact, there is already some suggestion in the literature that such tasks result in weakened or even *reversed* asymmetries in left handers.

The best example to date is from Gonzalez, Ganel, and Goodale (2006), who used a hand choice task which required participants to make jigsaw puzzles on a table. The midline of the table was marked so that participants' reaches could be coded as ipsilateral (on the same side of the table as the grasping limb) or contralateral (on the opposite side of the table to the grasping limb). It was found that right handers used their dominant hand for 78% of their reaches, whereas left handers used their "dominant" left hand only 48% of the time. In other words, as a group left handers had a slight tendency to choose to use their non-dominant hand.

In the first follow up experiment, Gonzalez, Whitwell, Morrissey, Ganel, and Goodale (2007) asked participants to make Lego™ constructions as well as jigsaw puzzles. They found that the left handers used their dominant hand only 44% of the time to pick up the Lego™ pieces, and on 49% of occasions to reach and grasp the puzzle pieces. Conversely, right handers used their right hand 82% of the time and 76% of the time for grasping Lego™ and puzzle pieces respectively. The implication here is that left handers use their non-dominant hand more often, and are not mirror images of right handers, which is contrary to findings in other experiments where right and left handers have displayed similar patterns of dominant hand choice (Bishop, Ross, Daniels & Bright, 1996; Bryden, Pryde & Roy, 2000; Calvert & Bishop, 1998).

Harris and Carlson (1993) performed a grasping choice experiment with a large number of dextral and adextral adults and children. Participants were required to pick up single objects with either hand either centrally or in left or right space, and then hand them to the experimenter. For central targets, the 40 dextrals and 40 adextrals were equivalent in their bias towards preferred hand use (77% in dextrals; 83% in adextrals). Hemispace, as in the Gonzalez and colleagues' tasks, biased participants towards ipsilateral hand use, but this effect only decreased dominant hand use by about 7-8% in contralateral space, equivalently in both groups.

Hand choice tasks were designed, in part, to demonstrate how willing participants are to use their non-preferred hand when it becomes more difficult for the preferred hand, typically by placing targets into peripheral space using some sort of horizontal array. For example, Bryden, Singh, Steenhuis & Clarkson (1994) designed elongated variants of a dot filling and a pegboard task, which required participants to use only one hand at a time starting from extreme left and extreme right-sided positions. The authors found, that left handers were significantly more left handed than right handers, and right handers were significantly more right handed than left handers. Unfortunately by analysing these data by left and right, rather than preferred and non-preferred hands, little could be concluded about strength of preference in these first hand choice tasks. (In other words, in an analysis of variance, when a factor "hand" is created by levels "left" versus "right", main effects and their associated interactions are difficult to interpret. Instead, if the question relates to right handers being more *one handed* then left handers, hand should instead have as levels "preferred" versus "non-preferred"). Steenhuis (1999) repeated these modified peg and dot filling tasks with larger samples. As in the earlier experiment, the supplied statistics are not particularly well suited to our research question here (at least in terms of the proportions of people who prefer their preferred hand in each handedness group). Nevertheless, the 52 dextrals and 48 adextrals did not differ significantly in terms of their *mean* magnitude of their *preferred hand* biases.

Calvert and Bishop (1998) extended earlier work by Bishop et al. (1996) on their own hand choice task, which seems to differentiate between strong and less strong right handers (as defined by questionnaire). They contrasted dextral and adextral groups on pointing to named locations, picking up cards and placing marbles, again utilising a horizontal array where less comfortable reaches across the body are required in contralateral space. They also argue that showing that dextrals and adextrals differ on this task is rather uninteresting, and that more stringent tests would be able to differentiate between subgroups of right handers, as theirs does (also see Bishop et al., 1996).

Between-participant variability can be a serious source of noise in studies of left-handed participants. For example, precise details of participant recruitment and selection are often sorely lacking. Smaller sample sizes can contribute to between study differences. In the experiments of Gonzalez and her colleagues (Gonzalez et al. 2006; 2007) the left-handed group was composed of either 10 or 11 participants In the Calvert and Bishop (1998) study 33 left handers were recruited but they were split into strong and mixed left-handed groups. Bryden and her colleagues (2000) utilised 25 left handers in their experiment. It is not clear from the methods sections of the early studies by Gonzalez and colleagues whether or not these samples (of left handers in particular) overlapped. Nevertheless, Gonzalez & Goodale (2009) report data from a later sample of 18 left- and 18 right handers obtained from the University of Lethbridge and found similar results for grasping biases in picking up Lego™ pieces[1]. They also claim that these asymmetries predict hemispheric lateralisation of speech and language as assessed using a dichotic listening test.

In the hand choice studies using elongated stimulus arrays, participants were constrained to use only one hand at a time. It may be that these kinds of constraints

[1] Later studies from the Lethbridge laboratory, published recently, also do not mention any overlap of samples from Gonzalez & Goodale (2009): Stone et al. (2013) and de Bruin et al. (2014).

influence hand choice, relative to other tasks where both limbs may move to distinct targets as in the Gonzalez puzzle and Lego tasks.

As a first step in reconciling these discrepancies in hand choice of left handers, we decided to use the Gonzalez et al. (2006) puzzle task with a larger sample of left- and right-handed individuals. We wanted to estimate what *proportions* of the participants (particularly in the left handed group) grasped more frequently with their right or left hand (as was done in the Gonzalez et al. 2007 and 2009 datasets). We also ran a second experiment with a another new set of left-handed participants**,** which investigated whether pointing, using only one hand or the other, rather than grasping, could discriminate between sub-groups of right and left handers.

2. Study 1

2.1. Method

2.1.1. Participants

A total of sixty-six Psychology undergraduates and members of the University's School of Psychology (23 males and 43 females, Mean age = 25.0) were recruited to take part in this study. We actively recruited participants who write with their left hand. In total, 33 were right-handed (7 male, 27 female), and 33 were left-handed (16 male, 16 female) as defined by handwriting hand. Some of the participants were level 1 undergraduates and received course credit for their participation. Participants' handedness was assessed using a 15-item abbreviated version of the Waterloo Handedness Questionnaire (WHQ; Steenhuis & Bryden, 1989, scores can range from -30 to +30). Sighting dominance was assessed using a variant the Miles A-B-C test (Miles, 1929), which requires aligning a distant target with a slot produced by two hand held cards at arms' length. Foot preference was determined by pantomiming kicking a ball. (Supplementary Table 1 displays the mean ages and WHQ scores, and foot and eye preference frequencies as a function of handedness). All participants reported normal or corrected to normal vision. Informed consent was obtained from all participants before completing this experiment. All procedures were approved by the School's Ethics Committee.

2.1.2. Stimulus Materials

Stimuli used were two different twenty-four piece jigsaw puzzles (each measuring 24 x 16.5 cm). Puzzle pieces were distributed equally on both sides of the midline. Puzzle 1 had pieces that were 3.75 x 4.25cm; puzzle 2 had pieces that were 6.25 cm^2. A large sheet of plain white card (84.1 cm x 59.4 cm) was used to make the puzzles on. Printed pictures of the puzzles were displayed on the midline above the white card for participants' reference. A video camera (Panasonic Mini DV NV-GS60) was used to film participants' hands and the workspace while completing the jigsaw puzzles.

2.1.3. Procedure

Participants were tested individually in 15 minute sessions. The WHQ was administered before beginning the puzzle task. Because handedness questionnaires can be highly subjective as they rely on participants' comprehension and memory (Bryden et al., 2000), participants were instructed to mime the actions in question so that a more accurate answer could be given. Scores were totalled and ranged from –30 to +30, where negative scores indicated left-hand preference and positive scores indicated right-hand preference.

For the puzzle task, participants were seated on an adjustable chair so that their midline was in line with the central join between the tables. The scrambled puzzle pieces and the associated printed picture were placed on the white card on the table. Participants were instructed to complete the puzzle as quickly as possible. A stopwatch was used to time participants performing this task, while the video camera filmed the participants' hands and workspace. The order in which participants completed the two puzzles was counter-balanced.

2.1.4. Coding

Using the video footage, all grasps of puzzle pieces were coded. Grasps were coded as dominant or non-dominant and ipsilateral (on the same side of the table as the grasping limb) or contralateral, as in Gonzalez et al. (2006).

2.2. Results

In the Gonzalez et al. (2006) study the data were analyzed using ANOVA with a factor called “hand and space”, which used the percentages of movements made for dominant hand ipsilateral, non-dominant hand ipsilateral, dominant hand contralateral, and non-dominant hand contralateral. For sake of comparison, the data are plotted following this convention in fig 1. However, it should be noted that the levels of the hand and space factor are not independent of one another, (i.e. if dominant contralateral percentages are increased, non-dominant ipsilateral movements must decrease, and so on). Even so, these data are really frequencies. Therefore planned chi square comparisons may have been appropriate. Nevertheless the crucial contrast is between the left handers' and right handers' tendency to use the dominant hand. Therefore we calculated dominant hand use percentages for each participant. The distributions for this measure were not particularly skewed (left-handed group skew=-0.795, SE=0.409; right-handed group skew=-0.314, SE=.409) or kurtotic (left-handed group kurtosis=-0.620, SE=.0409; right-handed group kurtosis=-0.907, SE=0.798). The variances of these two groups were also approximately equal (Levine's F=0.761, p=0.386 NS). Therefore we compared the group means using an independent samples t-test. The left-handed group's dominant hand use (63.7%) was not significantly less than the right-handed group's dominant use (70.9%; t(64)= -1.35; p=0.18). The two groups were not significantly different in dominant hand use even if, on the basis of Gonzalez et al.'s results, a one tailed prediction was made (p=0.09, one-tailed, N.S.). Both right and left handers made a similar number of total grasps across the two puzzles (mean grasps = 56 and 53, respectively).

Insert Fig. 1 about here

In their second and subsequent papers, Gonzalez et al (2007) reported how many left handers used their non-dominant hand more often than their dominant hand. On their variant of the puzzle task, 9/10 right handers used their dominant hand more often compared with 5 or 6/10 left handers using their dominant hand equally or more often (one person was very close to 50%). In contrast, 26 out of 33 (79%) of our left-handed participants used their dominant hand more often than they used their non-dominant hand. Similarly, 27 of 33 (82%) right-handed participants also used their dominant hand more often, illustrating the lack of asymmetries between our right- and left handers.

In some of the studies where the largest differences favouring right hander preferred hand movements were found (Gonzalez et al., 2006; 2007) strong left handers were used. In our study, we used handwriting hand for inclusion and opted for a larger sample size[2]. Of course in any sample of left-handed writers, handedness inventory scores will be much less skewed towards strong handedness than in any randomly selected group of right handed writers (e.g. Annett, 1967). Gonzalez and her colleagues actually report a cut-off score for inclusion in one of their papers, which was an EHI score of +70 or more for strong right handers and -70 or less for strong left handers (Gonzalez et al. 2006; note that in Gonzalez et al. 2007 although selection criteria were not reported, the mean Edinburgh Handedness Index score for the left-handed group was -94.6, suggesting very strong left handers indeed). On our modified Waterloo Handedness Questionnaire, an arithmetically equivalent score of + or – 21 was selected for inclusion in two strong handedness groups. Mean dominant hand grasping was even more left-handed in the strong left-handed group (n=19, 67.2%, compared with 63.7% when all left handers are included: n=33). Only a few right handers are excluded by this cut off -- they remain equivalently right handed in grasping choice (70.9%, n=28, an identical estimate to that from n=33). We also investigated patterns of hand use by separating our participants into strong and moderate right- and left-handed groups (defined by a median split of the WHQ scores). A one way ANOVA (repeated measures: hand and space; between-subjects factor: group) confirmed that there were no significant differences in hand use for the four groups of participants on all levels of the hand and space factor (all $F < 1.82$, all $p > .153$; see Fig. 2).

[2] In theory if strong handedness was an inclusion criteria, the cut-offs should have been established before testing. In addition, the number of people screened and how they were recruited should have been reported.

Insert Fig. 2 about here

2.3. Study 1 Discussion

These results suggest that right- and left-handed individuals are equivalently biased towards the dominant hand (71% and 64% respectively), superimposed on a generalised preference for ipsilateral movements (Gabbard & Helbig, 2004; Gardinier, Franco & Schieber, 2006). They do not replicate the findings of the relevant previous studies. On average, in two smaller samples of left and right handers grasping puzzle pieces, Gonzalez and colleagues find a right hander dominant hand bias of 77% and a left hander dominant hand bias of 46%.

We attempted to replicate the essentials of her design in our experiment. Twenty-four piece children's puzzles were used, although we required our participants to complete two puzzles rather than one. However, a paired-samples t-test on a selection of our participants confirmed that their dominant hand use did not differ between puzzle 1 and puzzle 2 ($t(24)=1.109, p=0.278$). Furthermore, there were no significant differences between right and left handers in time taken to complete puzzle 1 and puzzle 2, and they were highly correlated ($r = 0.823$, $n = 25$, $p < 0.001$).

In response to a previous version of this manuscript, a reviewer suggested that our task may not have had sufficiently precision requirements to elicit right hand grasp preferences in our left hander group, as Gonzalez and Goodale (2009) only found the right hand bias in the left-handed group when small LEGO pieces (6.5 cm x 3.2 cm x 2.0 cm) were required, compared to large ones (11.2 cm x 1.5 cm x 6.0 cm). They related these differences to the precision requirements of grasping, suggesting that whole hand grasping may be less lateralised. This account is interesting but debateable. First, their right handers had a mean right hand bias for even the large LEGO pieces (65.2% of grasps; although it was numerically smaller than that found for the small pieces (75%). In the left handers, dominant hand bias did not change as a function of their two stimulus sizes (54.3% for large pieces, 54.8% for small ones). The between group difference was significant for the small pieces but not the large ones. At best such data suggest an interaction between groups worthy of further explanation; at worst, they could be examples of limitations of traditional significance testing methods, as the difference is above chance in one condition and perhaps just below chance in the other. In any case, the change between large and small (if statistically significant) was in the behaviour of the right handers, and not the left handers.

Our puzzle pieces are comparable to those used in Gonzalez and colleagues earlier studies, where they report left handers grasping more frequently at a group level with their right hand. Arguably, for this class of grasping stimulus at least, the precision requirement is at least partly determined by the thin "height" of puzzle pieces when placed on a table. Although we did not formally count them, many grasps we scored from tape were made by index finger and thumb exclusively, or using three fingers. We think it unlikely that the precision requirements for picking up puzzle pieces explains that lack of a difference in our sample. The left handers in our study and those of Gonzalez were similarly aged university undergraduates who were naive with respect to the purpose of the experiment. Differences in degree of hand preference did not moderate the effects, in our sample at least. Sampling bias, from the more heterogeneous adextral population, is a probable explanation for these discrepancies.

Of course, an advantage of using the puzzle task in this way is that participants are typically attending to completion of the puzzle and not to which hand they will select to grasp a particular piece. Of course, both hands are active in the task as puzzle pieces placed in the workspace can be manipulated by either hand. One hand is frequently used to hold completed parts of the puzzle in the "active area" while the other manipulates the piece being added, etc. It is conceivable that some skilled actions being performed by one hand in the active area leads to selection of the other hand for reaching towards the next piece, etc. Movement sequences in this task, in spite of its' attractiveness, can be reasonably complex, including scanning eye and head movements that are one, two or even three steps in advance of the hand (cf Hayhoe, Droll & Mennie, 2007).

For these reasons we decided to re-examine right and left handers' selection biases in a slightly more constrained way; selecting which hand to use to make a single, discrete rapid aiming movement to one of two suddenly appearing targets. These experiments resemble in some sense previous grasping selection studies (e.g. Bryden et al., 1994: Bishop et al., 1996) where participant's movements were constrained to choosing one hand or the other. We attempted to extend those designs by trying to manipulate the magnitude of the dominant hand bias. We varied the stimulus onset asynchrony (SOA) between the targets on a particular trial, assuming that participants would be biased towards initiating a movement towards the target which appeared earlier (as suggested by Scherberger, Goodale & Andersen, 2003). Second, we manipulated the relative distances having to be moved by either hand on particular trial. We assumed that participants would tend to select the hand which would make the shorter of the two possible movements.

3. Study 2

3.1. Method

3.1.1. Participants

Forty-nine different undergraduates and members of the University's School of Psychology (15 males and 34 females) participated in Study 2. In total, twenty-six were right-handed, and twenty-three were left-handed. Year 1 participants (n = 31) were recruited through the University's Research Participation Scheme, and received course credit for participation. Members of staff, postgraduate students, and years 2-4 Psychology undergraduates were recruited through e-mail. Participants' handedness was assessed using our abbreviated version of the WHQ. An independent-samples t-test on the absolute WHQ scores indicated that there is a significant difference between the strength of handedness of right- and left handers ($t(47) = 2.66$, $p < 0.05$). Supplementary Table 2 displays the participants' mean ages and WHQ scores, as well as foot and eye preference frequencies as a function of handedness. As in study 1, all participants reported normal or corrected to normal vision. Informed consent was obtained from all participants before completing this experiment. All procedures were approved by the School's Ethics Committee.

3.1.2. Apparatus and Stimulus Materials

An in-house light-emitting diode (LED) grid (80 cm x 100 cm), and corresponding PC software were used to present pairs of red targets (6.5 cd/m^2) and a green central fixation point (7.5 cd/m^2), which appeared in line with the participant's midline. The hand that the participant used on each trial (dominant or non-dominant) and the side of space moved to as defined by the moving hand (ipsilateral or contralateral) were recorded.

3.1.3 Procedure

In testing sessions of approximately 30 minutes, participants completed the abbreviated WHQ, followed by the pointing task. The pointing experiment was conducted in a darkened laboratory to ensure that targets on the LED grid could be seen clearly without any interference from reflections or shadows. Participants were seated upright in an adjustable chair in front of the LED grid so that their midline was aligned with the centre of the grid. Participants began each trial with their index fingers positioned on pre-defined ‘home’ points 18 cm apart at the edge of the grid closest to their torso and centred relative to their body midline.

At the beginning of each trial, a green fixation light appeared in the centre of the grid for a random duration of between 700 ms and 1500 ms. Two red target lights were illuminated, one to the right of the midline and one to the left, as the fixation point was extinguished. The target lights remained visible for a duration of 400 ms. Participants were required to use the hand of their choice to point to only one of the targets on each trial as quickly and as accurately as possible. The target that was pointed to, and the hand that was used, were entirely decided by the participant. (Although we did not instruct participants explicitly on this point, they were permitted to reach across the midline to point to targets on the opposite side of the LED board). We provided no instruction requiring them to use both hands overall, although the task implicitly suggests that one hand should probably not have been used exclusively. The hand used and side of space moved to relative to the moving hand were recorded by the experimenter and the participant was subsequently instructed to return to the home points in preparation for the next trial.

Over a total of 80 trials, 16 target pairs were used, of which 8 were symmetrical and 8 were asymmetrical about the midline. Each different target pair appeared 5 times over the course of the experiment. The symmetrical target pairs were equidistant from both of the participants’ hands as well as equidistant from the fixation point. It was important that the targets were equidistant from the fixation point because reaction time varies as a function of eccentricity (Nazir & Jacobs, 1991). The asymmetrical targets were equidistant from the fixation point, but were different distances from the participants' right and left hands. Of these asymmetric target pairs, 4 created an affordance to use the right hand (because the right hand was closer to the target presented in right hemispace relative to the paired target presented in left hemispace) and 4 created a left hand affordance (see Fig. 3 below). In total, 20 trials created a right-hand affordance, 20 trials warranted a left-hand affordance, and 40 trials did not create any affordance. The most extreme affordance pairs were 15 cm from the start position of the closer hand and 45 cm from the more distant hand.

Insert Fig. 3 about here

A second manipulation entailed varying the stimulus onset asynchrony (SOA) so that one target appeared slightly before the other. Five different intervals were used: -60 ms (left target appeared 60 ms before the right target), -30 ms, 0, +30 ms and +60 ms. For each SOA there were 16 trials.

The targets were presented in a random order. All 80 trials were presented in one block, and each trial was manually initiated by the experimenter pressing a key. Participants were permitted rest breaks on request.

3.2. Results

3.2.1. Dominant Hand Use

For each participant a total of 80 unimanual hand movements were coded as dominant (using preferred hand) or non-dominant (using non-preferred hand). Each movement was also coded as ipsilateral or contralateral. Both the left-handed (M = 70.5%, SEM = 4.27) and right-handed participants (M = 74.8%, SEM = 2.10) were similarly biased to use their dominant hand. As in study 1, we also calculated the proportions of right and left handers that chose to point more frequently with their dominant or non-dominant hand. Eighteen out of 23 (78%) of our left-handed participants used their dominant hand more often than they used their non-dominant hand, while 25 of 26 (96%) right-handed participants used their dominant hand more often. However, an independent samples t-test, for which Levene's test verified that equal variances could be assumed ($F = 0.85$; $p > 0.05$), confirmed that the difference between the two handedness groups' dominant hand use was not significant ($t_{(47)} = 0.85$; $p > 0.05$, NS). Indeed, as depicted in Fig. 4, right- and left-handed participants used their dominant and non-dominant hands a similar number of times in both ipsilateral and contralateral space.

Insert Fig. 4 about here

3.2.2. Target Affordance

The position of the targets was manipulated in order to investigate whether participants were more influenced by their hand preference or the ease of movement required to point at the targets. A repeated measures 3 x 2 ANOVA was used to analyse the affordance data. *Affordance* was a within-subjects factor with 3 levels: dominant (one target in the pair presented closest to the dominant hand); equal (targets were equidistant from the hands), and non-dominant (one target was closer to the non-dominant hand). Handedness was a between-subjects factor with two levels (left-handed; right-handed, as determined by handwriting hand). Mauchly's test of sphericity revealed a significant result (chi-square = 30.26; $p < 0.05$), therefore Greenhouse Geisser (epsilon = 0.68) corrected degrees of freedom values are reported. A significant main effect of target affordance was found ($F_{(1.35\ 63.43)} = 104.40$; $p < 0.001$, Partial eta squared = 0.690, representing a medium effect size, Cohen, 1992), whereby dominant hand use was greatest for dominant affordances (M = 93.01%, SEM = 1.35), less for equal affordances (M= 77.80%, SEM = 2.81), and least for non-dominant affordances (M = 41.96%, SEM = 4.81). Post hoc pairwise comparisons, with the Bonferroni correction to the significance level applied, confirmed that the differences between each of the three affordance levels were significant ($p < 0.001$ for all comparisons). Fig. 5 illustrates the pattern of dominant hand use for right- and left handers across the affordance levels. There was no significant between-subjects effect of handedness ($F_{(1\ 47)} = 0.57$; $p > 0.05$, NS). Right- and left handers displayed similar dominant hand use to one another across each of the three affordance levels. There was no significant interaction between affordance and handedness ($F_{(1.35\ 63.43)} = 0.12$; $p > 0.05$, NS), which illustrates that both handedness groups displayed the same pattern of dominant hand use across all three affordance levels. Overall, the results of the ANOVA suggest that right-handed and left-handed participants are mirror images of one another (when left or right, rather than dominant or nondominant hands are considered, of course) with respect to the affordance manipulation.

Insert Fig. 5 about here

3.2.3. Stimulus Onset Asynchrony (SOA)

A repeated measures ANOVA was used. The within-subjects factor was *SOA* with 5 levels; 60 ms dom (the target on the side of the dominant hand appeared 60 ms earlier than the target on the side of the non-dominant hand), 30 ms dom, no SOA (both targets appear simultaneously), 30 ms non-dom (the target on the side of the non-dominant hand appeared 30 ms earlier than the target on the side of the dominant hand), 60 ms non-dom. The between-subjects factor was handedness. Mauchly's test of sphericity revealed a significant result (chi-square = 52.87; $p < 0.05$), therefore Greenhouse Geisser (epsilon = 0.59) correct values of degrees of freedom are reported. A significant main effect of SOA was obtained ($F_{(2.36\ 110.71)} = 57.78$; $p < 0.001$, partial eta squared = 0.551, representing a medium effect), whereby dominant hand use increased linearly as SOA was varied from 60 ms early on the dominant side to 60 ms early on the non-dominant side (See Fig. 6). These results suggest that participants were more likely to use their dominant hand when a target was presented early on their non-dominant side than on their dominant side, which is the opposite pattern to what had been expected. Post hoc pairwise comparisons, with Bonferroni correction applied, verified that the differences between all levels of SOA were significant ($p < 0.01$ for all comparisons). There were no significant between-subjects effects ($F_{(1\ 47)} = 0.794$; $p > 0.05$, NS). As can be seen from Fig. 6, for all levels of

SOA, right handers and left handers displayed similar percentages of dominant hand use. There was no significant interaction between SOA and handedness ($F_{(2.36\ 110.71)} = 57.78$; $p > 0.05$), which suggests that right-handed and left-handed participants were similarly influenced by the SOA manipulation in how often they used their dominant hand.

Insert Fig. 6 about here

3.2.4. Handedness strength and dominant hand use

Participants were classified as strong or moderate right- or left handers by a median split of the WHQ scores. A one-way ANOVA (dependent measure: dominant hand use; between-subjects factor: group) revealed a significant between-groups effect ($F_{(3\ 44)} = 7.97$; $p < 0.001$, Partial Eta Squared = 0.352, indicating a small effect size). Post hoc pairwise comparisons, using the Bonferroni method, revealed significant differences in dominant hand use between strong left handers (M = 83.09%, SEM = 4.50) and moderate left handers (M = 56.58%, SEM = 4.50; p = 0.001), and between strong right handers (M = 81.55%, SEM = 4.14) and moderate left handers (p = 0.001). However, the differences were not significant for any other combination of handedness groups. A further one-way ANOVA (dependent measure: hand and space; between-subjects factor: group) confirmed that differences in hand use between the handedness groups were only evident for moves with the dominant hand into ipsilateral space ($F (3\ 47) = 10.33$; $p < 0.001$) and for movements with the non-dominant hand in ipsilateral space ($F (3\ 47) = 4.71$; $p < 0.05$). These results appear graphically in supplementary Fig. 2.

3.2.5 Study 2 Discussion

In a forced choice pointing task, participants were required to make a rapid reaching movement to one of two possible targets. Our expectation was that (superimposed on a dominant hand bias, as seen in experiment 1 and the studies of Gonzalez and colleagues), without instruction to do so, participants would tend to make primarily ipsilateral movements (e.g. Gardinier et al. 2006) given their inertial properties (i.e. they are more effortful to start and to stop) relative to contralateral movements (Carey, Hargreaves & Goodale, 1996; Carey & Liddle, 2013**;** Carey & Otto-de Haart, 2001; Gordon, Gilhardi, Cooper, & Ghez, 1994) or for reasons of stimulus-response compatibility (Gabbard & Helbig, 2004; Rabbit, 1978; Rubichi & Nicoletti, 2006).

This exactly what participants did. As in our study 1, both right and left handers were equivalently biased towards selecting their dominant hand to point with (75% and 70.5% respectively), but that bias was somewhat reduced for movements towards targets on the opposite side of space.

4. Study 3

These hand choice studies have all been analysed, as in the current investigation, using null hypothesis significance testing. Cumming (2012; 2013) argues that using meta analysis to provide confidence intervals around an estimate provided a more accurate and interpretable picture then comparing separate studies which do or do not result in a statistically significant differences. Given the discrepancies between our results and those of others on hand choice, we decided that a random effects meta analysis might allow for an across-study estimate of the size of any difference between right handers and left handers on hand choice tasks, and would allow for 95% confidence interval construction based on between and within-study heterogeneity (see Carey & Johnstone, 2014, for a similar analysis on language laterality in left and right handers). Such approaches are useful for creating precise estimates of effects (and their likely range in the population; Cumming, 2012; Kline, 2004). “Fixed effects” models assume that each individual study is sampling the same underlying population effect, and that all of the between study differences are due to measurement noise, sampling error, subtle differences in instructions and so on. “Random effects” models do not assume that all of the underlying studies sample an identical population effect (Borenstein, et al. 2010; Cumming, 2012; Haddock, Rindskopf & Shadish, 1998); hence there are sources of variation (demand characteristics seem likely in some of the reaching across the midline sequential tasks, for example, or in our study 2) which will not be identical from study to study. One limitation of random effects methods, however, is that studies with smaller sample sizes can contribute more to the overall effect estimate, as they contribute more to estimates of between study variability (in fixed effects models smaller variances result in larger weights).

A "random effects" analytic strategy was used, given the differences in tasks used to estimate degree of hand choice. They all of course, differ on one or two salient dimensions. In the grasping choice studies such as the puzzle and Lego model paradigms described above, individuals are not constrained from using hands in close sequence or even simultaneously (see Stone et al., 2014, for experiments examining the "supporting role" of the non-grasping hand in these tasks). The hand choice experiments have also differed to varying extents in how handedness groups are defined or composed: for example, some sources create moderate left and moderate right handed groups symmetrically around zero points on their handedness questions, where following Kimura, we would classify many of these "moderate right handers" as adextral. In spite of these differences, these studies do have in common design features which provide equivalent affordances for either the right or the left hand. They do so by balancing target items around the body midline, controlling distances and so on.

4.1. Method

Studies where dextral and adextral samples were compared on movement choice tasks were selected, identified from databases such as Web of Science and Pubmed. Cited reference searches were particular useful in this instance as some of the earlier studies were published in the 1990s (e.g. Bishop et al., 1996; Bryden et al., 1994). MetaXL freeware (Doi et al., 2011; http://www.epigear.com/index_files/metaxl.html, based on the Stata™ implementation of meta analysis) was used to perform a weighted means meta analysis on identified studies. Obtained effects from each experiment were converted into a preferred hand percentage use score. In a few instances, standard deviations (necessary for the analysis) were estimated by two observers from published **figure** error bars (in such instances measurement error is presumably equivalent for the right- and left-handed group estimates in that particular study; for details see Supplementary materials "Study 3 Meta analysis of hand choice experiments"). Results are summarised graphically using a Forrest plot, and heterogeneity statistics Q and I^2 are also provided. If the **obtained differences are positively** signed (given the order of data entry, right handers preference score first) they indicate stronger dominant hand choice in dextrals. Furthermore, if the obtained CIs do not overlap zero (no difference), the analysis would strongly support previous studies suggesting weakened hand choice in adextrals, contrary to the present results.

4.2. Results – Study 3.

Fig. 7 is a Forrest plot of the random effects meta analysis.

Insert Fig. 7 about here

The results, unsurprisingly, suggest considerable heterogeneity in this literature, quantified by the significant Cochrane's Q statistic (76.52, $p<0.001$); which is a measure of the deviations of each studies' individual estimate from the overall estimate, weighted by their variability. Some experts suggest that I^2 is more appropriate, as it measures variability that is due to heterogeneity between studies**,** and not variance due to sampling error (Higgins, Thompson, Deeks, & Altman 2003). The obtained I^2 value of 78% suggests considerable between-study heterogeneity. In spite of these differences, the overall effect estimate of 12.51% (7.16-17.86% C.I.) supports the results of Gonzalez and colleagues (2006; 2007) and Brown, Roy, Rohr, & Bryden (2006). The overall mean difference estimate is a 12.5% larger bias in the dextral population. A fixed effects model suggests a slightly smaller overall weight mean (8.95%) and slightly smaller but similar Cis, which do not overlap with zero (6.53%-11:37%).

4.3 Discussion – Study 3.

This last analysis suggests that some aspects of our procedure, or sampling bias, resulting in a failure to detect a real difference between the right-handed and left-handed samples in both study 1 and study 2. Of course, some of samples in the meta analysis of study 3 may (and do) overlap, which might add to some of the heterogeneity obtained. In addition, the strongest weight means effects are largely from the LEGO puzzle making experiments, with the exception of Brown (2006), which utilised the “WatHand Cabinet Test” of Pamela Bryden and her colleagues, which requires several grasping tasks (some of which, as they acknowledge, require practiced actions after the grasp such as throwing, which is right hand lateralised in many left handers, see Peters, 1990). Many of the other hand choice tasks have stricter testing conditions which require the use of one hand at a time (such as our pointing task in study 2), which may lead, in some participants, to demand characteristics driving more equivalent use of both hands than might be the case **in** less constrained non-experimental conditions.

5. General Discussion

Our data do not suggest that left handers are less left handed than right handers. Although our sample size is comparable to many of the other hand choice studies reviewed above, the recent extensions of the Gonzalez puzzle/model paradigm using a distinct sample of left handers (Gonzalez & Goodale, 2009; Stone et al., 2013) suggests that using their paradigm the effects are reliably obtained. Curiously, for our study 1 in any case, there are very few obvious differences between our methods and theirs in terms of puzzle simplicity, number of trials, instructions to participants, and so on. Nevertheless the results of study 3 are supportive of their results.

One of the few remaining differences could be recruitment and selection of the left-handed participants. In our experiment, we used writing hand to define left and right handedness and did not select left handers matched for hand preference magnitude with the right-handed group. We did so because we were interested in obtaining a reasonably large sample, and because it is difficult to tease apart environmental influences from genetic/biological factors which push some left handers towards more ambidexterous hand preference (if not performance). In fact this dichotomous classification we adopt could be an issue for some people classified as right handed, as there remain in some cultures, even in the UK, an anti-sinistral bias against left-handed writing. However, re-classifying the participants into strong and moderate handedness groups by median split did not change the pattern of the data in either study 1 or study 2 (shown in Fig. 2 and supplementary Fig. 1).

We have extended the grasping hand selection paradigm to reaching in study 2. These data also suggest that left handers are as likely to choose their dominant hand as right handers, in a task where complementary actions of the non-chosen hand are never present (whereas in the puzzle task, both hands are often working simultaneously).

Although distance of the potential targets had predictable effects on hand choice, our SOA manipulation worked in a way opposite to what we predicted. It could be that salience of the latter target is greater given the timings used. Indeed, even in instances where participants engaged in some premotor processing relative to the first target, they may have been attracted to the second target pre-movement onset or in very early stages of the movement. It is well known that error correction for targets that jump after limb movement onset can happen in the absence of any conscious awareness of target or movement change (Goodale, Pellison & Prablanc, 1986). In any case, the absence of an obvious explanation for this effect is not overly relevant, as it was not different in right and left handers.

In the aiming task, participants were told to reach to one target as quickly as they could with the hand of their choice. Although 4 participants used only their dominant hand throughout that task (2 left handers and 2 right handers; fortuitously perhaps), most participants understood that the each hand should be used on some occasions. Nevertheless, we choose not to provide a more explicit instruction of this sort, because of a concern from pilot testing that individuals might adopt a cognitive strategy (like switching hands from trial to trial, deciding which hand to use before a target appeared, using short term memory to remember overall hand use, etc.) which might mask the more implicit biases towards the dominant hand which we hoped to obtain. We did interview participants post experimentally; the most commonly reported strategy was to “reach with the hand closest to the target”. These reports suggest that participants were selecting targets first and the hand to be used second, but if this explanation was accurate dominant hand biases would not be obtained. In fact, inspection of Fig. 5 suggests that the dominant hand bias is substantially larger than the bias provided by targets placed closer to the non-dominant hand. These data suggest that hand can be selected for early in the premotor period; nevertheless, target affordance can lead to 60-65% non-dominant hand use (relative to the 20-25% non-dominant hand use in the equal affordance conditions). In spite of this plasticity under more extreme affordances, left handers did not show significantly less dominant hand bias than right handers.

The differences between our experimental results here and the meta analysis suggest that further research is needed to identify the limits of the right hand bias (e.g. what tasks it is found in, test-retest reliability, and so on) and its' relationship to manual and functional asymmetries). The good news is that these techniques are relatively simple and inexpensive, and can be used with minimal instruction for participants of many ages and abilities. For example, some preliminary work (Sacrey, Arnold, Whishaw & Gonzalez, 2013) suggests that a right hand grasping bias emerges at the age of 4 or 5 years, although this particular study employed only ten right handed children in each age group, so further research is needed to firm up this intriguing conclusion (which could easily be contrasted with other milestones of behavioural asymmetry; Gentry & Gabbard, 1995; Scharoun & Bryden, 2014).

An appealing interpretation of the Gonzalez and colleagues results is that a right hand bias in left handers is related to the left hemispheric dominance expected in approximately 70% of any reasonably large sample. Our data are less suggestive of this particular type of task for predicting manual activity will predict left or right hemispheric dominance for speech and language. We acknowledge that Gonzalez and colleagues find their most dramatic effects using small LEGO pieces which may require greater precision of grasping in some ways than the puzzle pieces we use in study 1 (although one would hope, given the largely contralateral control of all fingers, that such as effect would be found for several types of grasping targets). Nevertheless, reaching grasping and aiming movements are only one class of manual behaviour - others may be better suited for language asymmetry prediction, in that they are more directly linked related to speech production.

6. Conclusion

Two separate studies, one on reaching and grasping and one on aiming choice do not support the suggestion that hand movement choice is biased towards the nondominant hand in adextrals**,** relative to well matched dextral participants. Nevertheless, a meta analysis of available hand choice studies suggest that adextrals are likely to be ten percent less handed than their dextral counterparts. Such data suggest that these types of hand choice may eventually provide a marker of underlying cerebral asymmetries.

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Fig. Captions

Fig. 1. Categorising the grasps as a function of hand used (dominant, non-dominant) and side of space as defined by the grasping hand (ipsilateral, contralateral). Mean percentages of the total number of movements made are depicted. The maximum percentage possible was 50 (as only half of the pieces were presented in either space). Participants have been classified as right or left handed by handwriting hand. Error bars show SEMs.

Fig 2. Categorising all grasps as a function of hand used (dominant, non-dominant) and side of space and handedness subgroup. Participants have been classified as strong or moderate right or left handed by a median split of the WHQ scores. Error bars show SEMs.

Fig. 3. Examples of target affordances. Pale grey dots represent pairs of targets and black dots represent the central fixation point. Top left: extreme left affordance (more likely to point to left target with left hand). Top right: extreme right affordance (more likely to point to right target with right hand). Bottom: Equal affordance, equidistant targets. Note: size of targets and fixation point are not to scale.

Fig. 4. . Categorising the 80 pointing movements as a function of hand used (dominant, non-dominant) and side of space moved to as defined by that hand (ipsilateral, contralateral) for right and left handers. Mean percentages of the total number of movements made are depicted. Error bars show SEMs. As in study 1, a bias to point with the dominant hand is superimposed on a bias to point ipsilaterally. Note that target affordance and the fact that two targets are always available on either side of the midline results in much stronger ipsilateral biases in this study compared with study 1.

Fig 5. Mean percentage of dominant hand use for each level of target affordance for right and left handers. Dominant indicates target was nearer to the participant's dominant hand. Error bars show SEMs.

Fig. 6. Mean percentage of dominant hand use across levels of SOA for right and left handers. Error bars show SEMs.

Fig. 7. Forrest plot of the random effects meta analysis on hand choice experiments, dextral preferred hand bias compared with adextral preferred hand bias. Individual study names appear in the leftmost column. WMD=weighted mean difference (positive values = right handers more biased towards using their dominant hand than the left handers). The size of each central square associated with a particular study indicates the % weight in the overall weighted mean estimate (also provided in the far right column). The dotted vertical line is the overall weighted mean estimate. The solid vertical line is equivalent to no numerical difference between dextrals and adextrals in terms of their preferred hand bias in hand choice. The centre of the diamond is the overall weighted mean; its width indicates the magnitude of the confidence interval. Study 1 and study 2 data from the present investigation are summarised in the 3rd and 4th from bottom studies in the figure.

Supplementary material

Supplementary Table 1. Mean age and Waterloo Handedness Questionnaire scores as a function of handedness group. Foot preference and eye dominance are given as frequencies of the total number of participants in each group. Note that one left hander reported that they use their left and right foot equally, therefore displayed no foot preference.

Supplementary Table 2. Mean age and Waterloo Handedness Questionnaire scores as a function of handedness group. Foot preference and eye dominance are given as frequencies of the total number of participants in each group.

Supplementary Fig. 1. Study 2. Categorising the 80 pointing movements as a function of hand used (dominant, non-dominant) and side of space as defined by that hand (ipsilateral, contralateral). Mean percentages of the total number of movements made are depicted. Participants have been classified as strong or moderate right- or left handers by a median split of the WHQ scores. Error bars show SEMs. As study 1, a bias to point with the dominant hand is superimposed on a bias to point ipsilaterally. Note that target affordance and the fact that two targets are always available on either side of the midline results in much stronger ipsilateral biases in this study compared with study 1.

Supplementary spreadsheet 1. Study 3 Meta analysis of hand choice experiments.