The relationship between lateralisation patterns from sequence based motor tasks and hemispheric speech dominance

Jessica C. Hodgson[a;] Daniel Richardson[b c] and John M. Hudson[b]

[a]Lincoln Medical School, College of Science, University of Lincoln, Lincoln LN6 7TS

[b]School of Psychology, College of Social Science, University of Lincoln, Lincoln, LN6 7TS

[c]Present address: St George's Medical School, University of London, London SW17 0RE

Corresponding Author
Jessica C Hodgson
Lincoln Medical School – Universities of Nottingham and Lincoln
University of Lincoln
Lincoln
LN6 7TS
UK
E-mail: jhodgson@lincoln.ac.uk

Abstract

Objective: Skilled motor praxis and speech production display marked asymmetries at the individual and the population level, favouring the right hand and the left hemisphere respectively. Theories suggesting a common processing mechanism between praxis and speech are supported by evidence that shared neural architecture underlies both functions. Despite advances in understanding the neurobiology of this left-hemisphere specialisation the cortical networks linking these two functions are rarely investigated on a behavioural level.

Method: This study deploys functional Transcranial Doppler (fTCD) ultrasound to directly measure hemispheric activation during skilled manual praxis tasks shown to be correlated to hemispheric speech lateralisation indices. In a new paradigm we test the hypothesis that praxis tasks are highly dependent on the left hemisphere's capacity for processing sequential information will be better correlated with direction and strength of hemispheric speech lateralisation

Results: Across two experiments we firstly show that only certain praxis tasks (pegboard and coin-rotation) correlated with direct measurements of speech lateralisation despite shared properties across all tasks tested. Secondly, through novel imaging of hemispheric activation during praxis, results showed that the pegboard differed in the lateralisation pattern created and furthermore that it was significantly related to speech laterality indices, which was not the case for either of the other two tasks.

Conclusion: These results are discussed in terms of a lateralised speech-praxis control mechanism and demonstrates that measurements of motor paradigms through the use of fTCD are reliable enough to provide a new insight to the behavioural relationship been speech and handedness.

Key Words:

Motor Praxis

Speech Production

Cerebral Lateralisation

Functional Transcranial Doppler (fTCD)

Sequencing

Public Significance Statement:

It is well known that the left side of the brain plays an important role in the function of both speech and fine motor movement. This study shows that the brain activity produced by motor tasks that require sequential processing occurs predominantly in the left-hemisphere of the brain, irrespective of which hand is used. The study also showed that this is a similar pattern of brain activity seen in speech production tasks. This suggests that the two functions may rely on similar neural networks, which increases our understanding of how the two functions interact in the brain, and how they may sub serve each other in recovery from injury to this brain region.

1. Introduction

Skilled motor praxis and the capacity for language production have been described as the two defining characteristics of the human species (Corballis, 2010). Both functions display marked asymmetries at the individual and the population level, favouring the right-hand and the left-hemisphere respectively (McManus, 2002; Knecht et al., 2000a, b). Strong left-hemisphere asymmetry for language processing is a robust finding across methodologies (e.g. Costafreda et al., 2006; Dehaene-Lambertz et al., 2006; Knecht et al., 2000a, b) and similarly, the cortical activation patterns of manual praxis, that is, the ability to generate, coordinate and perform complex gestures and intentional actions, also reveal a left-hemisphere bias (Buxbaum et al., 2005; Haaland et al., 2004; Goldenberg, 2013). Despite advances in understanding the neurobiology of this left-hemisphere specialisation for fine motor action (Verstynen et al., 2005; Serrien et al., 2006) and speech production (Sahin et al., 2009; Flinker et al 2015) the cortical networks linking these two functions are rarely investigated on a complex behavioural level, for example by using praxis tasks commonly used in neuropsychology to determine motor-skill and handedness. This is predominantly due to constraints from these complex motor tasks inducing unacceptable movement artefacts in commonly used neuroimaging techniques, like fMRI, rendering exact simulations of neuropsychological assessments of motor-skill tasks unfeasible.

The association between praxis and language is longstanding in neuropsychology, with evidence revealing that left-hemisphere lesions often lead to combined impairments in motor control and speech processing (Rasmussen and Milner, 1975; Goldenberg, 2013) and that children with developmental language learning impairments often also present with impaired praxis skills (Redle et al., 2014; Hill, 2001). Evidence suggests that both speech and action involving fine motor control of the hands rely on common neural architecture (Vingerhoets et al., 2013); classic frontal-temporal speech production areas, namely the pars opercularis (PO) and pars triangularis (PT), are activated during motor tasks (Binkofski and Buccino, 2004) and motor cortex and pre-motor areas are active during language tasks (de Lafuente and Romo, 2004). These findings underlie the hypothesis that both functions share a common evolutionary origin specifically that spoken language may have evolved from gestural communication (Corballis, 2003; Arbib, 2000, 2005).

Such neurological overlap between praxis and speech is hypothesised to result from the two functions relying on similar processing mechanisms as well as shared architecture. One suggestion is that tasks which rely on sequential processing to execute complex actions will make use of similar cortical networks, independent of modality, and will predominantly lateralise to the left-hemisphere (e.g. Flowers and Hudson, 2013; Grimme et al., 2011). The left-hemisphere is recruited for complex sequential processing in a range of cognitive domains, and has been shown to be specifically involved in visuomotor control of action (Verstynen, et al., 2005) as well as being crucial sequential properties of language (Sahin, et al., 2009). Furthermore, left-hemisphere pathways activate more strongly than right-hemisphere homologues during complex fine motor tasks, regardless of the hand that is moving or the participant’s handedness (Haaland, et al., 2004; Serrien et al., 2006). It has also been demonstrated that handedness tasks involving fine motor sequencing are related to the direction of hemispheric lateralisation of speech activation (Gonzalez and Goodale, 2009; Hodgson and Hudson, 2016) and even that performance differences between the hands on skilled motor tasks can predict direction of language lateralisation, as measured by the Wada procedure (Flowers and Hudson, 2013).

What has not yet been measured, however, is the extent to which left-hemisphere speech regions are active during complex motor-skill tasks more commonly associated with measurements of praxis or handedness. Behavioural imaging paradigms that have attempted to address this have been limited to discreet button presses or finger tapping tasks (e.g

Haarland, et al., 2004; Verstynen et al., 2005) due to the confounds created by deploying more complex motor tasks in neuroimaging techniques (like fMRI) through unacceptable signal-to noise artefacts created from the excess movement, or incompatibility of praxis task equipment with the scanner. Paradigms using button presses or finger movements are arguably oversimplifications of the complexities of manual praxis underlying theories of motor and speech development (Corballis, 2010). Furthermore, despite agreement that sequential processing may be key to revealing the links between hemispheric specialisation for speech production and skilled motor praxis (Hodgson, Tremlin and Hudson, 2019; Hsu and Bishop, 2014; Grimme et al., 2011), previous studies examining this relationship use tasks which fail to effectively tap into this mechanism (e.g. Groen, et al., 2013).

The first experiment in this study was designed to probe this hypothesised left-lateralised preference for sequential processing, by correlating performance across a range of skilled praxis tasks with direct measurements of hemispheric speech lateralisation. A range of tasks was necessary to assess whether additional component processes may contribute to the successful execution of complex motor tasks, in addition to sequencing. Task selection was based upon identifying other candidate cognitive/behavioural elements that may relate strongly to speech lateralisation. These additional processes can be categorised as follows: 1) Precision grip and release and grip strength; this skill is crucial in determining an individual's ability to pick up the pegs smoothly and accurately and release them as fast as possible. Evidence suggests that precision grip is one of the later aspects of hand manipulation skills to develop in young children (Scharoun and Bryden, 2014) and it has also been demonstrated that tasks which require use of the pincer grip motion are performed more accurately with the dominant hand (Gonzalez, Ganel and Goodale, 2006). A study by Annett, Annett, Hudson and Turner (1979) using stop-motion video analysis demonstrated that participants who had slower movement times on a pegboard task actually deployed a less effective release motion of the peg, but were comparable on other aspects of the grasp action. 2) Finger dexterity; this skill involves the ability to quickly and accurately manipulate the fingers into different positions and move individual digits at varying speeds and angles, as required by the task. Models of corticomotoneuronal pathways indicate that crucial rostrocaudal connections which project bilaterally from the brain stem are heavily involved in finger dexterity, and severing these connections at various points limits digit mobility to varying degrees of severity (Isa, Kinoshita and Nishimura, 2013). 3) Arm movement; skilled manual tasks often require an element of upper arm motion especially if the task involves crossing the midline of the body. This additional element of gross motor function involves separate muscle and nerve groups which may vary the pattern of hemispheric activity. 4) Psychomotor speed; this function is defined as the ability to maintain focus on a task requiring manual/motor response by accurately integrating relevant cognitive processes. It relies heavily on aspects such as working memory, attention and other ‘top-down’ processes to maintain motor speed and concentration on a specific task. Patients with deficits in regulation of psychomotor speed have been shown to have lesions extending bilaterally through parietal and temporal regions (Goldenberg, 2013). Experiment 1 deconstructed these factors into separate tasks and then correlated left- and right-hand performance across these tasks with separately derived speech lateralisation indices.

The second experiment then deployed a novel imaging paradigm using functional Transcranial Doppler ultrasound (fTCD) to derive lateralisation indices of *motor action* during three selected tasks. The use of fTCD in lateralisation research is well established (e.g. Aaslid et al., 1982; Deppe et al., 2004; and for a visual demonstration of the technique see Bishop et al., 2010) and has important methodological benefits over other imaging modalities. For example, it can be easily applied to clinical groups unable to undergo more invasive scanning procedures and is also appealing to developmental populations due to its unintimidating protocol. Previous work on imaging the motor cortex via fTCD has deployed simple finger tapping tasks to activate contralateral motor pathways as an indicator of functional relocalisation in stroke patients with aphasia and/or apraxia diagnoses (Silvestrini et al., 1993). Uomini and Meyer (2013) used fTCD to explore hemispheric activation of motor action and word generation during an archaeological study of stone tool use, and found correlations between the profile of motor activation and speech lateralisation. However the measurement of motor lateralisation using fTCD has not yet been applied to motor praxis tasks as used in neuropsychological assessments, or those known to correlate with speech laterality profiles (Hodgson et al., 2016). It was hypothesised that the tasks which correlate more strongly with speech lateralisation scores in experiment 1 will also display an increased left-hemisphere activation bias for both hands (contralateral activation for right-hand motion and ipsilateral activation for left-hand motion), in comparison to a baseline task in experiment 2. In addition it was hypothesised that derived motor lateralisation indices with a strong left-hemisphere bias would be more accurate predictors of degree of speech lateralisation indices. This would indicate that task-specific motor activation links to speech activation, which would provide insight to the component processes underlying both functions.

2. Experiment 1

2.1 Methods

2.1.1. Participants

Forty adults aged between 18 and 40 years (17 males; mean age: 20.07yrs; SD age: 3.7) were recruited from the University. Participants gave informed consent prior to taking part in the study. All participants had normal, or corrected to normal, vision and none had history of neurological disorders or trauma, or any condition known to affect the circulatory or central nervous systems. All participants were Caucasian and had English as their first language. They received research credits in return for their participation. The study received ethical approval by the School of Psychology Research Ethics Committee, University of Lincoln. Participants completed a shortened version of the Edinburgh Handedness Inventory to determine their self-reported hand preference (see Flowers and Hudson, 2013), which revealed that 6 of the 40 participants were left handed, denoted by a handedness quotient at or below zero.

2.1.2 Motor Skill Tasks

All participants performed 6 separate manual praxis tasks. The ordering of task presentation was counterbalanced between participants. Each task was performed with both hands, alternating between right and left on each trial, with the self-reported preferred hand going first on each task. Table 1 shows how each task corresponds theoretically to the component processes involved in skilled praxis tasks.

Task 1. Electronic Pegboard – This procedure has been described in detail in Hodgson and Hudson (2016). In brief, 20 pegs (6mm diameter × 24mm long) were moved one at a time from a row of holes on one side of a rectangular board to a row of holes at the opposite side of the board. The pegboard consisted of a 280 × 100 × 20mm board with two rows of 20 holes (7mm diameter) drilled 13mm apart along the length. The distance between the two lines of holes was 70mm. The Fitts' (1954) Index of Difficulty (Id) measurement for this board was Id = 7.6, making it unlikely that the task can be performed by pre-programmed aimed movements, and must involve some “online” movement control where handedness differences are most consistently found (Annett, Annett, Hudson, & Turner, 1979; Flowers and Hudson, 2013). This task was performed 3 times with each hand, as fast as possible, and exact timings (in milliseconds) were measured by the electrical circuitry hidden in the board.

Task 2. Coin-Rotation – Participants were asked to rotate a British two pence coin (diameter = 25.9 mm, thickness = 1.85 mm, weight = 7.12 g) as quickly as possible with their thumb, index, and middle fingers. The action required participants to turn the coin over 180° repeatedly, just using the fingers mentioned above. The time to perform 20 half turns was measured. The experimenter counted and timed the turns. This was performed 3 times with each hand. Performance was measured in seconds. This task has previously been shown to accurately measure manual dexterity in healthy adults (Mendoza et al., 2009) and patient groups (Heldner et al., 2014).

Task 3. Finger Tapping – Participants placed both hands flat on the table in front of them and were required to tap their index finger 10 times as fast as possible, whilst keeping their other fingers in contact with the table surface. This was performed 5 times with each hand. Taps were recorded by the experimenter and performance was measured in seconds.

Task 4. Pen and Paper Dotting – This task was designed as a pen and paper version of the pegboard. Participants were asked to hold a short felt tip pen in a pincer grip and place a single dot inside circles laid out in two rows on a piece of paper. They were instructed to do this as fast as possible and be as accurate as possible. The dimensions of the two rows of dots matched exactly the dimensions of the pegboard (see above) and the ordering of trial completion was also the same. Occasions where the dot was not inside the circle were classed as errors. Three trials were performed with each hand and the mean time and accuracy scores were calculated.

Task 5. Peg Placing – Participants were required to place 20 identical pegs from a pot positioned at the side of a board into 5 cups arranged on the board. The cups were placed in a circle in grooved slots to ensure the exact dimensions were consistent across participants. Participants were instructed to ensure all 20 pegs were sorted as fast as possible and they were explicitly told not to place into the same pot on two consecutive pegs, or to use an adjacent pot to the one just selected on consecutive pegs. These rules were to avoid participants placing into each pot in a circular manner or just making use of one pot.

Task 6. Grip strength – This static measurement was included as an alternative measure for hand preference, having previously been shown to effectively discriminate between preferred and non-preferred hand performance (Petersen et al., 1989). This was included as the hand preference questionnaire administered was based on self-report. Grip was assessed using a handheld dynamometer. Participants were required to sit with their feet flat on the floor and their arm at a comfortable right angled position by the side of their body. They were instructed to squeeze the device as hard as they could for 2 seconds and then release their grip. This was performed 3 times with each hand. Performance was measured in Kilograms.

[INSERT TABLE 1 HERE]

2.1.3 Speech Laterality

Cerebral blood flow velocity (CBFV) was measured via functional transcranial Doppler (fTCD) ultrasound whilst participants completed a word generation task. This task involved the silent production of words corresponding to a stimulus letter displayed on a computer screen. The paradigm has been described in detail elsewhere (Knecht et al., 2000a; Hodgson and Hudson, 2016) but briefly, participants receive a 5 s ‘clear mind’ message before a stimulus letter is displayed on the screen. At this point participants are asked to begin word generation silently until they see the next instruction to repeat the words they were just thinking of out loud. This is followed by a 35 s rest phase. The task has been well used in language lateralisation studies (Deppe et al., 2000; Knecht et al., 1998; Knecht et al., 2000a) and is known to reliably elicit hemispheric activation. Measurements of middle cerebral artery blood flow velocity during the periods of silent word generation are compared with the rest phase of the trial. Participants performed 23 trials with a different letter presented each time. Speech laterality indices were derived for each participant by taking the mean difference between left- and right-sided activity within a 10 sec window (see Woodhead et al., 2018 for explanation), from the period of interest which occurred 5-15secs after the start of each trial. The period of interest mean was then compared to the baseline rest phase extracted from the period -10 – 0 s during each epoch. Epochs last for 1 minute, from -10 s to 50 s. Speech laterality was assumed to be clear in all cases in which the LI deviated by > 2 SE from 0 (Knecht et al., 2001). Left-hemisphere or right-hemisphere speech dominance was indicated by positive or negative indices respectively. Cases with an LI < 2 SE from 0 were categorised as having bilateral speech representation.

2.2 Procedure

2.2.1 Motor Skill Tasks

Performance on 5 of the 6 motor tasks (Pegboard; Coin-rotation; Dotting; Finger Tapping; Peg Placing) was measured by the speed with which the tasks were completed. Mean movement times were calculated for preferred and non-preferred hand performance. For the sixth motor task, Grip Strength, performance was measured by the mean force squeezed in kilograms, for the preferred and non-preferred hands. Correlation coefficients were generated for the mean scores for each hand, across each task, and the data were then entered into a principal components analysis to identify common factors underpinning the performance differences.

2.2.2 Functional Transcranial Doppler

Speech lateralisation indices were derived from measurements of cerebral blood flow velocity (CBFV) taken from bilateral insonation of the middle cerebral arteries whilst participants performed the word generation task. Recordings were made with a commercially available system (DWL Doppler-Box^{TM}X: manufacturer, DWL Compumedics Germany GmbH) via a 2-MHz transducer probe attached to an adjustable headset, positioned over each temporal acoustic window. PsychoPy Software (Pierce, 2007) controlled the word generation experiment and sent marker pulses to the Doppler system to denote the onset of a trial. Data were analysed off-line with a MATLAB (Mathworks Inc., Sherborn, MA, USA) based software package called dopOSCCI version 2 (see Badcock, Holt, Holden and Bishop, 2012 for a detailed description).

2.3 Results

2.3.1 Motor Skill Tasks

To assess the relative hand performance across each task non-parametric tests were deployed due to non-normally distributed data. Wilcoxon signed rank tests were performed to examine differences between the preferred and non-preferred hand performance across each of the 6 tasks. Four of the tasks revealed significant differences between preferred and non-preferred hand skill. The preferred hand (PH) demonstrated greater proficiency than the non-preferred hand (NPH) on the Pegboard, (PH median = 23.1 s vs. NPH median = 23.9 s; Z = -2.55, p < .02, r = -.29); coin-rotation (PH median = 15.2 s vs NPH median = 17.9 s; Z = -5.12, p < .001, r = -.57); dotting task (PH median = 22.26 s vs. NPH median = 26.02; Z = -5.44, p < .001, r = -.61) and grip strength measurements (PH Median = 26 kg vs. NPH median = 24.8 kg; z = -2.64, p < .01, r = -.29). There were no significant differences between the hands on the placing task (PH Median = 35.3 s; NPH Median = 35.8 s; Z = - .66, p = .51) or the finger tapping task (PH Median = 1.78 s; NPH Median = 1.77 s; Z = -.96, p = .34). See table 2 for mean performance scores.

[INSERT TABLE 2 HERE]

2.3.2 Speech Laterality

Speech Lateralisation indices were obtained for 34 of the 40 participants. Six cases were unusable due to excess variability in the individual epoch recordings such that they had less than 50% acceptable trials recorded. LI values ranged from 3.79 to -2.36 (mean = 2.31, SD = 1.8) with 4 cases classed as atypically lateralised (i.e. had right-hemisphere or bilateral language distribution). Mean number of words generated per trial at the group level was 4.6 (SD= .066). In order to assess the relationship between speech laterality and the performance on the motor-skill tasks correlation coefficients were generated for each task and each hand against the speech LI scores (see Table 3). These indicate that only the Pegboard and Coin-rotation tasks correlated significantly with Speech LI scores.

[INSERT TABLE 3 HERE]

2.3.3 Factor Analysis

Initially, the data from the performance of the right- and left-hands across the 6 skill tasks was examined for its suitability to be included in the factor analysis. Several well recognised criteria for the factorability of a correlation were used. Firstly, it was observed that all 12 items correlated at least .3 with at least one other item, suggesting reasonable factorability. Secondly, the Kaiser-Meyer-Olkin measure of sampling adequacy was .61, above the commonly recommended value of .6, and Bartlett’s test of sphericity was significant ($\chi2$ (66) = 464.16, p < .001). The diagonals of the anti-image correlation matrix were also all over .5. Finally, the communalities were all above .3, further confirming that each item shared some common variance with other items. Given these overall indicators, factor analysis was deemed to be suitable with all items.

Principal components analysis was used because the primary purpose was to identify the factors underlying the relationship between the motor-skill tasks used. Initial eigen values indicated that the first four factors explained 40.4%, 18.8%, 13.2% and 10.8% of the variance respectively. Factors 5 to 12 had eigen values under one, and cumulatively explained 17% of the variance. Solutions for three and four factor models were each examined using varimax rotations of the factor loading matrix. The three factor solution, which explained 73.2% of the variance, was preferred because of: (a) the tasks included in this solution were similar to one another in terms of properties; (b) the 'levelling off' of eigen values on the scree plot after three factors; and (c) the two tasks included in the final component of the 4 factor solution were grip strength for right and left hands respectively, meaning that grip must represent distinct component of handedness, not directly relevant to the function of praxis ability/motor skill. See table 4 for results.

[INSERT TABLE 4 HERE]

2.4 Summary

Experiment 1 correlated behavioural performance on 6 different praxis tasks, selected due to shared component processing, with speech lateralisation indices derived using fTCD. Factor analysis revealed that the best fitting model included three separate component processes to describe the relationship between handedness performance measures. Scrutiny of the handedness tasks contributing to each factor (see table 4), and cross refencing with the processing requirements of each task (see table 1), indicates that the three components could be labelled as follows:

Component 1: Psychomotor speed. The majority of the tasks contributed to this factor, suggesting it most closely relates to the elements of visual and cognitive attention, required to carry out these motor actions efficiently, which we term psychomotor speed.

Component 2: Finger dexterity/ Arm movement. The two tasks which contribute to this factor (finger tapping and peg-placing) are those which require some degree of arm or hand movement as their main mode to completion. The movements of these two tasks are fairly rhythmic, and they are less complex to perform under time constraints.

Component 3: Sequencing. Only two tasks contributed to this factor, but they both involve a high level of visual and motor coordination, including cognitive control and precision placing and timing to follow the correct task pattern and most efficient route to completion of the movement. This concurs with evidence that sequential movements are more complex, and thus may be distinct from other types of motor action.

Following on from this it could be suggested that Component 3, sequencing, was most indicative of the type of action underlying speech and motor interactions seen in the literature. This was supported by the correlational analysis, which indicated that the two motor-skill tasks which contributed to Component 3 were also the tasks which correlated well with speech scores; pegboard task and coin-rotation, for both left- and right-hand movement. To explore the activation patterns created by these tasks this in greater depth, and to assess whether the sequencing component of these tasks is driving the connection between speech and motor action we conducted a second experiment. Experiment 2 was designed to assess the relationship between the hemispheric lateralisation indices created by different praxis tasks; whether these indices would be hand dependant, and finally, whether these indices could be significantly related to lateralisation patterns created by speech. The study was designed to obtain direct physiological measurements of hemispheric laterality during motor tasks, as well as during speech production, to compare hemispheric dominance between the hands and across functions.

3. Experiment 2

3.1 Methods

3.1.1 Participants

These were 23 adults aged 18-27 (5 males; mean age = 19.2; SD age = 1.92). 19 were right-handed, 3 left-handed and one individual was mixed handed, as measured by a handedness inventory (Flowers & Hudson, 2013). Participants satisfied the same criteria for inclusion as Experiment 1 and were recruited similarly.

3.1.2 Motor Skill Laterality Measurements

Two of the motor tasks from Experiment 1 were selected to form the experimental conditions in Experiment 2; the Pegboard and Coin-rotation. These tasks were chosen as they were the only ones to significantly correlate with speech lateralisation indices for both the right- and left-hand in the previous study, indicating that they may best tap into the common processing mechanisms underlying speech and praxis. A third task from Experiment 1, Finger tapping, was selected to serve as a control condition. A new paradigm was developed in order to measure the relative hemispheric activation during performance of these three motor tasks. Participants were seated at a computer screen with their hands placed on marked areas on the table in front of them. They were then instructed to keep absolutely still and not move their hands from the designated area until instructed to by the computer. A Psychopy software (Pierce, 2007) controlled computer program then ran the paradigm. Epochs lasted for 30 seconds each. This consisted of a pre-action ‘get ready’ phase (0 -3 s), followed by a 12 s ‘move’ phase (3 – 15s), where the instruction of either ‘Left’ or

‘Right’ was given indicating the participants should start performing the task with the corresponding hand. These direction prompts were displayed in a randomly generated order, but always consisted of 15 ‘right’ trials and 15 ‘left’ trials, totalling 30 trials per task. This was followed by a final rest phase (15 – 30 s) to allow the CBFV to return to baseline. The tasks were presented in a block design, the order of which was counterbalanced between participants.

The task formats were controlled to correspond with the fTCD paradigm, which meant that participants performed the action for 12 seconds and then stopped. The Finger Tapping control condition was performed exactly as described in Experiment 1 (see 2.1.2) using the second digit (index finger) only. The Coin-rotation was set up so that the 2 pence coin was placed in between the marked areas where the hands were resting. At the instruction of either ‘Left’ or ‘Right’ the participant was required to pick up the coin with the corresponding hand, and rotate it as many times as possible within the 12 s window. The Pegboard task was the most adapted from the original version described in Experiment 1. In this paradigm only half the pegs on the board were used (10 in total) and the board was positioned ipsilateral to the moving hand on each trial. This was done to ensure that the board did not cross the participants’ midline, to minimise movement of the upper arm as this could confuse the laterality measurement (the board was repositioned on each trial by the experimenter via sliding it between the pre-designated placement areas).

3.2. Data Analysis - Motor fTCD

Motor lateralisation indices were derived from measurements of cerebral blood flow velocity (CBFV) taken from bilateral insonation of the middle cerebral arteries whilst participants performed the three motor tasks described in 3.1.2. A set of 6 laterality indices (LI) was derived for each participant corresponding to left and right hand movement across each of the three tasks. These indices were calculated by extracting information from the Psychopy (Pierce, 2007) program to denote which of the 30 epochs were the 'left' and which were the 'right' trials, which were subsequently matched up to the LI values produced from the analysis. Following the method set out in Woodhead et al. (2018), as with the speech paradigms, the LI values were calculated from the mean difference between left and right hemisphere activity within the 10sec period of interest (POI) in each trial. In the present paradigm the POI was taken from the 'move' phase of the paradigm which was 5 – 15 s following onset of the trial. The baseline period was taken from the 'rest' phase.

Motor laterality was assumed to be clear in all cases in which the LI deviated by > 2 SE from 0 (Knecht et al., 2001). Left-hemisphere or right-hemisphere motor dominance was indicated by positive or negative indices respectively. Cases with an LI < 2 SE from 0 were categorised as having bilateral motor representation. Participants required a minimum of 15 acceptable trials (i.e. 50%) to be included in the analysis. Criteria for acceptable trials were those which maintained a consistent insonation signal throughout the whole epoch capture, (i.e. didn't contain any drop in signal), or those which did not include any behavioural variation from the task (i.e. where the participants stopped, or dropped equipment). Although this 50% threshold was chosen arbitrarily, all participants well exceeded this threshold, and only 1 was excluded for behavioural reasons (dropped peg). Evoked flow plots showing the mean signal pattern from the left and right hemisphere channels during an epoch, are firstly displayed across tasks (see Figure 1) and then separated by task and hand (see Figure 2).

[INSERT FIGURE 1 HERE]

[INSERT FIGURE 2 HERE]

3.3 Speech Laterality

Speech lateralisation indices were obtained for each participant following completion of the motor paradigm. Participants performed the word generation paradigm, the overview of and outline of the fTCD analysis procedure for this task was identical to that described in Experiment 1 – see section 2.1.3

3.3 Statistical analysis

Initially LI scores were derived from each motor task, for each hand. This data was then analysed using paired sample t-tests for each task to measure differences between the hemispheric lateralisation indices produced between the left- and right-hands, at the group level. Variables were then entered into a repeated measures ANOVA, with a 2-way within subjects variable of 'hand' (left and right) and a 3-way within subjects variable of task (coin, tapping and pegboard), and between subjects variables of hand preference and speech laterality group (right and left).

3.3 Results

3.3.1 Lateralisation of Motor Skill Tasks

One participant was excluded from the analysis as their LI scores did not meet the quality thresholds required during pre-processing analysis and too many trials were unusable (for further detail on the processing steps involved see Badcock et al, 2012). Split half reliabilities of the odd and even epoch LI values were calculated for the left- and right-hand trials, across each of the three tasks. Pearson correlations indicated medium internal reliability in each of these calculations (see Table 5). To assess whether LI scores were significantly different to zero, thus indicating lateralised hemispheric activation, one-sample T tests were conducted (see table 6). This showed that at the group level all tasks exhibited lateralised activation patterns (either to left or right hemisphere), except the left-hand Pegboard task and the right-hand coin rotation task, which both displayed bilateral activation patterns.

[INSERT TABLE 5 HERE]

[INSERT TABLE 6 HERE]

To assess the interaction between ‘task’ and ‘hand used’ a two-way repeated measures ANOVA was conducted using the variables ‘Hand’ (2 levels; left and right) and ‘Task’ (3 levels; coin-rotation, Finger tapping and Pegboard). Results showed that there was a significant interaction between hand used and task performed ($F(2,40) = 4.01$ $p < .05$, $\eta_p^2 = .17$). This interaction effect shows that the laterality indices produced by the left- and right-hand were significantly different across the tasks performed (see Figure 3).

Following the significant interaction, simple main effects were calculated with a Bonferroni correction applied. Results show that there was a statistically significant simple main effect of hand used ($F(1,20) = 161.4$ $p < .0001$, $\eta_p^2 = .89$) across each of the motor tasks (Pegboard: mean difference of -2.13 between left and right hand LI scores (95% CI, -2.59 to -1.67); Coin Rotation: mean difference of -2.39 between left and right hand LI scores (95% CI, -3.06 to -1.72); Finger Tapping: mean difference of -3.2 between left and right hand LI scores (95% CI, -3.97 to -2.46), which indicates that the lateralisation indices derived from the left and right hands significantly differ in direction regardless of task.

There was also a significant simple main effect of task ($F(2,40) = 9.41$ $p < .0001$, $\eta_p^2 = .32$) demonstrating a difference between the hemispheric lateralisation indices depending on the task that was being performed. Scrutiny of the pairwise comparisons for each task show that there were significant differences in the LIs between the pegboard and coin rotation tasks for the left-hand (a mean difference in LI score of 1.31 (95% CI, .32 to 2.29) and the right-hand (a mean difference in LI score of 1.05 (95% CI, -.03 to 2.12). There were also significant differences in the LIs between the pegboard and finger tapping tasks for the left hand (a mean difference in LI score of 1.63 (95% CI, .56 to 2.68), but these were not significant for the right hand (a mean difference in LI score of .54 (95% CI, -.37 to 1.45). Comparisons between the coin rotation and finger tapping task LIs were not statistically significant for either the left (a mean difference in LI score of .32 (95% CI, -.46 to 1.11) or right (a mean difference in LI score of -.50 (95% CI, -1.34 to .33) hands.

[INSERT FIGURE 3 HERE]

3.3.2 Speech Lateralisation

The word generation task produced the expected left-hemisphere dominant LI value across the sample as a whole; LI mean = 2.03, SD = 1.76. The range of mean LI scores was -2.65 to 4.67, and there were 2 individuals who were right-hemisphere lateralised (mean LI scores of -2.65 and -1.98 respectively) and 2 classed as bilateral (mean LI scores of .61 and .95). Split half reliabilities of the odd and even epoch LI values are shown in Table 5, and one-sample T tests showing lateralised hemispheric activation are shown in Table 6.

3.3.3 Predictive Relationship Between Speech Lateralisation and Motor Lateralisation

To assess the predictive relationship between the speech indices and the indices from the motor tasks, multiple regression was conducted using the stepwise entry method with mean speech lateralisation indices as the dependent variable. The mean lateralisation indices derived from the three praxis tasks by each hand were all entered as predictor variables. From this analysis a significant regression model was produced (see Table 7 for regression statistics), which explains 22% of the variance in speech lateralisation indices. Both of the models included only lateralisation indices from the right hand of the pegboard task and excluded each of the other task/hand combinations, indicating that the specific processing requirements in the pegboard task are most similar to those underlying speech production. Correlations of the LI values from each motor task, for each hand, and the Speech LI scores also reveal that only the right-hand of the pegboard task significantly correlated to the Speech score (see Table 8). Figure 4 plots the relationship between the mean speech indices derived from the word generation task and the mean motor indices derived from the pegboard task for the right hand.

[INSERT FIGURE 4 HERE]

[INSERT TABLE 7 HERE]

[INSERT TABLE 8 HERE]

4. Discussion

Theories suggesting a common processing mechanism between praxis and speech are supported by evidence that shared neural architecture underlies both functions (e.g. Binkofski and Buccino, 2004). This relationship is rarely investigated on a complex behavioural level using neuroimaging, due to the movement artefacts necessarily created by standard neuropsychological praxis tasks. This study makes use of an emerging technique in cognitive neuroscience, fTCD, to investigate the hemispheric specialisation underlying lateralised behaviour. Across a set of two experiments the hypothesis that motor praxis and speech share cortical networks as both are reliant on complex sequential processing controlled by the left-hemisphere was investigated in an overt paradigm (e.g. Grimme et al, 2011; Flowers and Hudson, 2013). In Experiment 1 performance on the pegboard task and five additional motor-skill tasks sharing common processing requirements were compared to speech lateralisation indices derived from a word generation task during fTCD ultrasound. Results indicated that only two of the six motor tasks correlated significantly with speech LI scores; the pegboard and the coin-rotation task. A factor analysis model confirmed that only these two tasks contributed to the best fitting model to explain the shared components across all of the handedness tasks.

These tasks were then used in Experiment 2 with an fTCD motor paradigm to derive lateralisation indices during movement of the left- and right-hands. This second experiment demonstrated that the right-hand activated the contralateral (left) hemisphere for the pegboard task, but not the coin rotation task (which displayed bilateral activation), whereas the left-hand activated the right hemisphere during the coin rotation task, but not the pegboard task, which produced bilateral activation. This was compared to a control condition task of finger tapping, with a single digit (index finger), during which both hands activated the contralateral hemisphere. In addition, a good proportion of the variance in speech lateralisation indices could be predicted by the motor indices produced from the right hand of the pegboard task. Together these data provide good evidence that the inherent properties within sequencing-based praxis tasks are more linked to speech processing than a non-complex motor task such as tapping, and that they are represented more strongly in the left hemisphere.

The validity of the tasks chosen as effective skill-based motor activities for measuring hand performance was demonstrated as each were accurate in distinguishing the dominant hand, although in two of the tasks this difference was not significant (Placing Task and Finger Tapping). If hand performance had differed in direction, rather than just degree, across each of these tasks then it would be concerning for the subsequent comparisons with speech indices in terms of making assumptions about the hemispheric control of each task. There were however some unexpected findings from the results between speech and motor performance across the 6 tasks. The first observation of interest was that the pen and paper version of the pegboard; the Dotting task, did not significantly correlate with speech laterality, despite it appearing as primary factors in the first component of the factor analysis. This lack of relationship with speech indices is surprising because the only component it did not share with the pegboard was the grip and release mechanism of picking up the pegs (participants kept a constant hold of the pen during this task). Therefore this is an indicator that the sequential movement and manipulation of the fingers in the pegboard task may be a key factor regarding its common processing with speech. Support for this is provided by data from fMRI of finger movement tasks which show increased left-hemisphere activation during sequential and non-sequential finger movements (Hayashi, et al., 2008).

The second observation from comparisons of each of these tasks is that the placing task did not correlate well with speech indices, or indeed with many of the other motor tasks. This is likely due to the parameters of the task, as observations of participant behaviour during task execution suggested that it was more cognitively demanding than the other, more purely motor, comparators. For example, often participants hovered over a pot whilst deciding whether it would constitute an illegal move on that trial, before then making the peg placement. Thus it is clear that the task involved a greater working memory component than the other tasks, as well as a greater requirement for effective response inhibition. Such mechanisms are known to be controlled predominantly by the right-hemisphere (Aron, Robbins and Poldrack, 2014), and so it is likely that a reduced left-hemisphere network would be involved, even in right-hand movement, thus reducing its relationship with speech indices. This however means it was a successful choice as a task in terms of one which eliminated motor sequencing, however it was perhaps not as comparable with the other handedness tasks in terms of measuring a component of motor skill (as it seemed to rely on more cognitive motor planning mechanisms).

Experiment 2 demonstrated that the patterns of hemispheric activity resulting from motor skill tasks varied depending on how speech-related the tasks were. Two tasks were tested based on factor analysis from Experiment 1 indicating that they share common components, the pegboard and the coin-rotation task, along with a third task, finger tapping, which showed to load on a distinct component in the factor analysis, and so was used as a control condition. Results confirmed the hypothesis that greater left-hemisphere activation would be seen in the experimental tasks regardless of the hand that is moving, although this was more pronounced for the Pegboard task than the coin-rotation task. This is a novel finding as it demonstrates the left-hemisphere bias for motor sequencing tasks in real time, and is an indicator as to why links between speech laterality and pegboard performance have been found previously (Flowers and Hudson, 2013; Hodgson and Hudson, 2016). Furthermore the fTCD data has been shown to be reliable in this new paradigm, which suggests that the activation patterns seen are representative of motor networks. It should be noted however, that reliability measures in fTCD studies are frequently high, and so this paradigm may benefit from inclusion of additional trials per participant in future studies, to see if reliability can be increased even further. It may be that in motor paradigms participant fatigue becomes an issue with maintaining performance consistency, which could also impact on results if too many trials were included. These issues could be explored in future studies of motor action measured by fTCD.

Figure 5 is a schematic representation of the results presented in Experiment 2. It indicates that in the control condition, finger tapping, predominantly contralateral activation was displayed, evidenced by the strong connections between each opposing hemisphere and hand. Weak ipsilateral networks are represented in order to account for the fact that some epochs present this type of activation (i.e. the LI is a mean score), which suggests that both hemispheres are working to greater or lesser degrees in support of task execution. This is the case across each task shown in Figure 5. The Coin-rotation task is represented by less strong contralateral activation and an increased role for the left hemisphere ipsilateral network, to reflect the mean LI scores being close to zero. Finally the pegboard task is represented by increased contralateral activation compared to the coin-rotation task, but is also supported by much more activation in the left hemisphere ipsilateral network. This representation is supported by evidence indicating ipsilateral control exhibits a functional asymmetry between hemispheres whereby activation in left motor cortex during left-handed movements is stronger than activation in right motor cortex during right-handed movements (Van den Berg, Swinnen and Wenderoth, 2011; Hayashi et al., 2008; Kobayashi, Hutchinson, Schlaug and Pascual-Leone, 2003).

[INSERT FIGURE 5 HERE]

Differences in the characteristics of the three motor tasks imaged require consideration. One of the factors inherent in the pegboard task is the reliance on visual processing in order to successfully complete the task. This differs from the requirements of the coin-rotation and the finger tapping, where visual feedback does not inform the continuation of the motor action in the same way. For example, participants often reported it was easier to complete the finger tapping and the coin-rotation by fixating the gaze at a point away from their hands. Due to the size of the pegs and holes of the pegboard task, it would not be possible to complete it accurately without the integration of visual information. Visual feedback has been shown to be integral to successful execution of handedness tasks (Smith, McCrary and Smith, 1960; Miall, Weir and Stein, 1985), and the disruption of accurate visual feedback during the grooved pegboard task has been show to neural processing speed and considerably impair performance (Fujisaki, 2012). Lateralisation of visuospatial control has reliably been shown to produce a right hemisphere bias (e.g. Whitehouse and Bishop, 2009; Flöel et al., 2001), which would not account for the predominant left hemisphere activation pattern seen in the pegboard task, which is more visually dependent than others in this study. However evidence from grasping studies altering the visual properties of the target reveal that visuomotor mechanisms encapsulated in the left hemisphere play a crucial role in the visual control of action (Gonzalez, Ganel and Goodale, 2006), thus supporting the notion that the pegboard is more heavily dependent on sensory processing streams which also make use of specialised left hemispheric networks. In addition the lateral arm movement required in the pegboard task is greater relative to the two other conditions. Although this was minimised in Experiment 2 by reducing the length of the board from 20 down to 10 pegs, and by positioning the board on the ipsilateral side of space, some increased arm and shoulder movement remained. Evidence from studies of cerebral lateralisation of arm movement control suggest that each hemisphere activates a specialised system of control, resulting bilateral activation is at different stages of the movements (Mutha, Haaland and Sainburg, 2013). If this is the case, then it seems unlikely that excess arm movement will have impacted significantly on the laterality pattern, as predominant left hemisphere activation, rather than bilateral, was found in the pegboard task.

An interesting finding from the regressions analysis of speech LI scores and motor LI scores from experiment 2, was that only right-hand pegboard lateralisation indices were significant predictors of speech lateralisation scores, with left-hand indices from the Pegboard approaching significance. None of the other motor-skill task indices were significant predictors of speech indices. This could be explained by the presence of a theoretical lateralised praxis centre model, which makes use of strong contra-lateral connections between the left-hemisphere and right-hand, and makes additional use of ipsilateral connections between left-hemisphere and hand when performing complex tasks. Such a model has been proposed by Hodgson and Hudson (2018; see also McManus et al., 2016) based upon the differential performance of the hands across skilled motor tasks. Such models suggest that although the contralateral pathways for control of the hands are still activated during handedness tasks, it could be that a specialised region in the left hemisphere, a so called 'praxis centre', mediates the control of this system in complex tasks. Hodgson and Hudson (2018) argue that extent of left hemispheric control of motor output is potentially determined by the complexity of the motor task. For complex movements requiring sequential timing, visuomotor control and accurate integration of visual feedback the use of a lateralised praxis centre may be required, which is typically in the left-hemisphere. They suggest the praxis centre model can explain why non-preferred hand performance is usually worse, as it is said to rely on an 'inherently nosier' motor centre in the right-hemisphere, which is dependent on transfer of information via the corpus callosum for control of the left hand. The data in the current study could extend that theory by integrating speech processing into such a model. A left lateralised speech-praxis centre model proposes that the left-hemisphere 'centre' activated by speech and praxis functions on a computational basis of integration between 'areas' or 'sets' of neural connections involved in the processing of key functions including; motor action, visuo-motor control, motor planning, phonological and auditory processing and sequential control of complex 'higher order' operations. Evidence from TMS studies lends support to this notion, for example it has been shown that the optimal site to elicit motor evoked potentials (MEPs) for the ipsilateral hand are in areas slightly lateral and ventral to the site of maximal contralateral MEP (Ziemann, et al., 1999). This shift in location within the left-hemisphere for control of ipsilateral relative to contralateral hand movements has also been shown using neuroimaging (e.g. Cramer, et al, 1999). Furthermore recent evidence demonstrates that even within Broca's area, the region classically thought of as the heart of speech production and, crucially, an area which is confined to a specific part of the left hemisphere, there are spatially and temporally separate processes which occur to support speech (Flinker et al., 2015; Sahin et al., 2009). Therefore a revised model of speech and praxis argues that the interconnectedness of these functions will determine the efficiency with which the left-hemisphere is able to support motor control of both hands as well as speech production processes. The data presented here is currently not sufficient to address this theory, but future work developing the paradigm used here to measure speech related motor praxis activation using fTCD could extend this theory further, especially in terms of the characteristics expected during typical and atypical development.

5. Limitations

Although the data presented here demonstrate that variations in hemispheric activation across motor praxis tasks exist, it is important to note the limitations of the current study. Firstly, the initial analysis linking motor-tasks with speech LI scores is correlational, therefore it could be argued that the selection of the pegboard and coin-rotation tasks was relatively arbitrary. Secondly, whilst experiment 2 did show the predictive nature of the motor task lateralisation indices on speech indices, it is not possible to draw conclusions about underlying neural architecture based on these data alone. Instead the data can only be used to make assumptions that may prove useful in shaping future research paradigms investigating the relationship between speech and motor-skill.

6. Conclusions

These studies demonstrate that the relationship between speech and motor networks can be investigated with a behavioural imaging paradigm, hereby bridging the practice-imaging gap, by integrating praxis tasks typical to neuropsychological assessments of motor function, with tasks optimised for imaging paradigms. The data suggest that the relationship between left-hemisphere involvement in motor-skill tasks is mediated by the components of the task, and that where these components are complex and sequential in nature, and thus resemble speech production, there will be overlap in the activation patterns observed. This has implications for the design of future studies which should aim to explore the component processing of motor-skill activation further, and should explore whether lateralisation patterns are consistent within individuals, across tasks and across modalities from an imaging perspective.

6. References

Annett, J., Annett, M., Hudson, P. T. W., & Turner, A. 1979. The control of movement in the preferred and non-preferred hands. Quarterly Journal of Experimental Psychology, 31:641-652

Arbib, M.A. 2000. The Mirror System, Imitation, and the Evolution of Language. In Nehaniv, C. & Dautenhahn, K., editors. Imitation in Animals and Artifacts. Cambridge MA: MIT Press.

Arbib, M. A. 2005. From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. Behavioral and Brain Sciences, 28:105-

124.

Aron, A., Robbins, T. & Poldrack, R. 2014. Inhibition and the right inferior frontal cortex: one decade on. Trends in Cognitive Sciences, 18:177-185. http://dx.doi.org/10.1016/j.tics.2013.12.003

Badcock, N. A., Holt, G., Holden, A., & Bishop, D. V. 2012. dopOSCCI: A functional transcranial doppler ultrasonography summary suite for the assessment of cerebral lateralisation of cognitive function. Journal of Neuroscience Methods, 204:383-388.

Binkofski, F. & Buccino, G. 2004. Motor functions of the Broca's region. Brain and Language, 89:362-369

Bishop, D. 2013. Cerebral asymmetry and language development: cause, correlate, or consequence? Science, 340:1230531. doi: 10.1126/science.1230531

Buxbaum, L.J., Kyle, K.M., & Menon, R. 2005. On beyond mirror neurons: internal representations subserving imitation and recognition of skilled object-related actions in humans. Brain Res Cogn Brain Res., 25:226–239. doi:10.1016/j.cogbrainres.2005.05.014

Corballis, M. C. 2003. From mouth to hand: Gesture, speech, and the evolution of right-handedness. Behavioral and Brain Sciences, 26:199-208

Corballis M.C. 2010. Handedness and Cerebral Asymmetry. In Hugdahl, K. & Westerhausen, R., editors. The Two Halves of the Brain; Information Processing in the Cerebral Hemispheres. Cambridge MA: MIT Press, pp 65-88

Costafreda, S., G , Fu, C. H. Y., Lee, L., Everitt, B., Brammer, M., J, & David, A., S. 2006. A systematic review and quantitative appraisal of fMRI studies of verbal fluency: Role of the left inferior frontal gyrus. Human Brain Mapping, 27: 799-810

Dehaene-Lambertz, G., Hertz-Pannier, L., Dubois, J., Mériaux, S., Roche, A., Sigman, M., & Dehaene, S. 2006. Functional organization of perisylvian activation during presentation of sentences in preverbal infants. PNAS, 103: 14240-14245. doi: 10.1073/pnas.0606302103

de Lafuente, V. & Romo, R. 2004. Language abilities of motor cortex. Neuron 41:178-180

Deppe, M., Knecht, S., Papke, K., Lohmann, H., Fleischer, H., Heindel, W., . . . Henningsen, H. 2000. Assessment of hemispheric language Lateralisation; a comparison between fMRI and fTCD. Journal of Cerebral Blood Flow & Metabolism, 20:263-268

Fitts, P. M. 1954. The information capacity of the human motor system in controlling the amplitude of movement. Journal of Experimental Psychology, 47:381–391. doi:10.1037/h0055392

Flinker, A., Korzeniewska, A., Shestyuk, A., Franaszczuk, P., Dronkers, N., Knight, R., & Crone, N. 2015. Redefining the role of Broca's area in speech. PNAS, 112:2871-2875. doi/10.1073/pnas.1414491112

Flöel, A., Knecht, S., Lohmann, H., Deppe, M., Sommer, J., Drager, B., et al. 2001. Language and spatial attention can lateralize to the same hemisphere in healthy humans. Neurology, 57:1018-1024

Flowers, K. & Hudson, J. 2013. Motor laterality as an indicator of speech laterality. Neuropsychology, 27:256-65. doi: 10.1037/a0031664.

Fujisaki, W. 2012. Effects of delayed visual feedback on grooved pegboard test performance. Front Psychol., 3: 61. doi 10.3389/fpsyg.2012.00061

Goldenberg, G. 2013. Apraxia: the cognitive side of motor control. Oxford, UK; Oxford University Press

Gonzalez, C., Ganel, T., & Goodale, M. 2006. Hemispheric Specialization for the Visual Control of Action Is Independent of Handedness. Journal of Neurophysiology, 95:3496-3501. DOI**:** 10.1152/jn.01187.2005

Gonzalez C. L., & Goodale M. A. 2009. Hand preference for precision grasping predicts language lateralization. Neuropsychologia, 47:3182–3189. 10.1016/j.neuropsychologia.2009.07.019

Grimme, B., Fuchs, S., Perrier, P., & Schöner, G. 2011. Limb versus speech motor control: A conceptual review. Motor Control, 15:5-33.

Groen, M., Whitehouse, A., Badcock, N. & Bishop, D. 2013. Associations between Handedness and Cerebral Lateralisation for Language: A Comparison of Three Measures in Children. *PLoS ONE, 8*:e64876. doi:10.1371/journal.pone.0064876

Haaland, K., Elsinger, C., Mayer, A., Durgerian, S. & Rao, S. 2004. Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralisation. J. Cogn. Neurosci., 16:621-636.

Hayashi, M. J., Saito, D. N., Aramaki, Y., Asai, T., Fujibayashi, Y., & Sadato, N. 2008. Hemispheric asymmetry of frequency-dependent suppression in the ipsilateral primary motor cortex during finger movement: A functional magnetic resonance imaging study. Cerebral Cortex, 18:2932–2940

Heldner, M., Vanbellingen, T., Bohlhalter, S., Mattle, H., Müri, R. & Kamm, C. 2014. Coin rotation task: a valid test for manual dexterity in multiple sclerosis. Phys Ther., 94:1644-51. doi: 10.2522/ptj.20130252

Hill, E.L. 2001. Non-specific nature of specific language impairment: a review of the literature with regard to concomitant motor impairments. Int. J. Lang. Comm. Dis., 36:149–171

Hodgson, J. C., Hirst, R. J., & Hudson, J. M. (2016). Hemispheric speech lateralisation in the developing brain is related to motor praxis ability. *Developmental cognitive neuroscience*, *22*, 9–17. https://doi.org/10.1016/j.dcn.2016.09.005

Hodgson, J & Hudson, J. 2018. Speech lateralization and motor control. Progress in Brain Research, 238: 145-178, https://doi.org/10.1016/bs.pbr.2018.06.009

Hodgson, J & Hudson, J. 2016. Atypical language lateralisation in developmental coordination disorder. Journal of Neuropsychology, DOI: 10.1111/jnp.12102

Hodgson, J, Tremlin, R. & Hudson, J. 2019. Disrupting the speech motor network: exploring hemispheric specialisation for verbal and manual sequencing using a dual-task approach. Neuropsychology, 33:1101-1110. doi: 10.1037/neu0000589.

Isa, T., Kinoshita, M. & Kishimura, Y. 2013. Role of direct vs. indirect pathways from the motor cortex to spinal motoneurons in the control of hand dexterity. Front. Neurol., 4; 191, http://dx.doi.org/10.3389/fneur.2013.00191

Knecht, S., Deppe, M., Ebner, A., Henningsen, H., Huber, T., Jokeit, H., & Ringelstein, E. 1998. Noninvasive determination of language lateralisation by functional transcranial doppler sonography A comparison with the wada test. Stroke, 29: 82-86.

Knecht, S., Deppe, M., Dräger, B., Bobe, L., Lohmann, H., Ringelstein, E., & Henningsen, H. 2000a. Language lateralisation in healthy right-handers. Brain, 123:74-81. doi: 10.1093/brain/123.1.74

Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., . . . Henningsen, H. 2000b. Handedness and hemispheric language dominance in healthy humans. Brain, 123: 2512-2518. doi: 10.1093/brain/123.12.2512

Knecht, S., Dräger, B., Flöel, A., Lohmann, H., Breitenstein, C., Deppe, M., . . . Ringelstein, E. 2001. Behavioural relevance of atypical language lateralisation in healthy subjects. Brain, 124:1657-1665.

Kobayashi, M., Hutchinson, S., Schlaug, G., & Pascual-Leone, A. 2003. Ipsilateral motor cortex activation on functional magnetic resonance imaging during unilateral hand movements is related to interhemispheric interactions. Neuroimage, 20:2259–2270.

McManus, I. C. 2002. Right Hand, Left Hand: The Origins of Asymmetry in Brains, Bodies, Atoms and Cultures. London: Weidenfeld and Nicholson.

McManus I. C., Van-Horn, J. D., & Bryden, P. 2016. The Tapley and Bryden test of performance differences between the hands: The original data, newer data, and the relation to pegboard and other tasks. Laterality: Asymmetries of Body, Brain and Cognition, 1-26. DOI: 10.1080/1357650X.2016.1141916

Mendoza, J., Apostolos, G., Humphreys, J., Hanna-Pladdy, B. & O'Bryant, S. 2009. Coin Rotation Task (CRT): A New Test of Motor Dexterity. Arch Clin Neuropsychol, 24: 287-292. doi: 10.1093/arclin/acp030

Miall, R. C., Weir, D. J., & Stein, J. F. 1985. Visuomotor tracking with delayed visual feedback. Neuroscience 16:511–520

Mutha, P. K., Haaland, K. Y., & Sainburg, R. L. 2013. Rethinking Motor Lateralization: Specialized but Complementary Mechanisms for Motor Control of Each Arm. PLoS ONE, 8: e58582. doi:10.1371/journal.pone.0058582

Peirce, J. W. 2007. PsychoPy—psychophysics software in python. Journal of Neuroscience Methods, 162: 8-13.

Petersen, P, Petrick, M., Connor, H., & Conkilin, D. 1989. Grip strength and hand dominance: challenging the 10% rule. Am J Occup Ther. 43:444-7

Rasmussen, T., & Milner, B. 1975. Clinical and surgical studies of the cerebral speech areas in man. Cerebral localization. Massachusetts: Springer. pp. 238-257

Redle, E., Vannest, J., Maloney, T., Tsevat, R., Eikenberry, S., Lewis, B. … & Holland, S. 2014. Functional MRI evidence for fine motor praxis dysfunction in children with persistent speech disorders. Brain Research, 1597: 47-56. doi.org/10.1016/j.brainres.2014.11.047 0006-8993

Sahin, N., Pinker, S, Cash, S, Schomer, D. & Halgren, E. 2009. Sequential processing of lexical, grammatical, and phonological information within Broca's area. Science, 326:445-9, DOI. 10.1126/science.1174481

Scharoun, S. & Bryden, P. 2014. Hand preference, performance abilities, and hand selection in children. Frontiers in Psychology, 5:82, doi: 10.3389/fpsyg.2014.00082

Serrien, D., Ivry, R. & Swinnen, S. 2006. Dynamics of hemispheric specialization and integration in the context of motor control. Nature Reviews Neuroscience, 7:160-166

Silvestrini, M., Caltagirone, C., Cupini, L., Matteis, M., Troisi, E., & Bernardi, G. 1993. Activation of Healthy Hemisphere in Poststroke Recovery: A Transcranial Doppler Study. Stroke, 24:1673-1677. doi: 10.1161/01.STR.24.11.1673

Smith, W. M., McCrary, J. W., & Smith, K. U. 1960. Delayed visual feedback and behavior. Science, 132:1013–1014

Uomini N.T. & Meyer G.F. (2013) Shared Brain Lateralization Patterns in Language and Acheulean Stone Tool Production: A Functional Transcranial Doppler Ultrasound Study. PLOS ONE 8(8): e72693. https://doi.org/10.1371/journal.pone.0072693

Van den berg, F., Swinnen, S. & Wenderoth, N. 2011. Involvement of the Primary Motor Cortex in Controlling Movements Executed with the Ipsilateral Hand Differs between Left- and Right-handers. Journal of Cognitive Neuroscience 23: 3456–3469

Verstynen, T., Diedrichsen, J., Albert, N., Aparicio, P., & Ivry, R., 2005. Ipsilateral Motor Cortex Activity During Unimanual Hand Movements Relates to Task Complexity. J Neurophysiol 93:1209-1222. doi:10.1152/jn.00720.2004.

Vingerhoets, G., Alderweireldt, A., Vandemaele, P., Cai, Q., Van der Haegen, L., Brysbaert, M., & Achten, E. 2013. Praxis and language are linked: Evidence from co-lateralisation in individuals with atypical language dominance. Cortex, 49: 172-183. doi:10.1016/j.cortex.2011.11.003

Whitehouse, A. J. & Bishop, D. V. M. 2009. Hemispheric division of function is the result of independent probabilistic biases. Neuropsychologia, 47, 1938-1943. doi: 10.1016/j.neuropsychologia.2009.03.005

Woodhead, Z., Rutherford, H. A., & Bishop, D. (2018). Measurement of language laterality using functional transcranial Doppler ultrasound: a comparison of different tasks. *Wellcome open research*, *3*, 104. https://doi.org/10.12688/wellcomeopenres.14720.3

Table 1. Theoretical overview of the how each task relates to component processes of the Pegboard.

	Sequencing	Finger Dexterity	Psychomotor speed	Grip and Release	Arm Movement
Electronic Pegboard	X	X	X	X	X
Coin Rotation	X	X	X	X	
Peg Placing			X	X	X
Pen and Paper Dotting	X		X		X
Finger Tapping		X	X		
Grip Strength				X	

Table 2. Performance data for the 6 hand-skill tasks, means and standard deviations. PH = Preferred Hand; NPH = Non-Preferred Hand

	Mean	**Standard deviation**
Peg Placing PH (secs)	35.11	4.59
Peg Placing NPH (secs)	35.43	4.35
Peg Board PH (secs)	22.96	1.91
Peg Board NPH (secs)	23.76	2.73
Finger Tapping PH (secs)	1.89	.3
Finger Tapping NPH (secs)	1.88	.3
Pen & Paper Dotting PH (secs)	22.79	3.59
Pen & Paper Dotting NPH (secs)	26.9	5.33
Coin Rotation NPH (secs)	15.57	2.84
Coin Rotation PH (secs)	17.92	4.10
Grip Strength PH (kg)	27.64	8.81
Grip Strength NPH (kg)	26.4	9.51

Table 3. Spearman's Rho values for the LI scores from the 6 hand skill tasks and the speech LI scores from Experiment 1. * indicates p < 0.05; ** indicates p < 0.01

	Motor Task	**Speech LI score**
Preferred Hand (Mean LIs)	Pegboard	-.35*
	Dotting	-.13
	Peg Sorting	-.23
	Coin Rotation	-.49**
	Grip	-.01
	Finger Tapping	-.13
Non-Preferred Hand (Mean LIs)	Pegboard	-.43*
	Dotting	-.05
	Peg Sorting	-.32
	Coin Rotation	-.42*
	Grip	.04
	Finger Tapping	-.18

Table 4. Factor loadings and communalities based on a principal components analysis with varimax rotation for 10 items (mean task performance scores used). PH = Preferred Hand; NPH = Non-Preferred Hand

	Component 1	**Component 2**	**Component 3**	**Communalities**
Peg Placing PH	.906			.84
Peg Placing NPH	.875			.84
Peg Board PH	.644		.483	.76
Finger Tapping NPH		.931		.91
Finger Tapping PH		.883		.84
Pen & Paper Dotting PH	.614	.662		.86
Pen & Paper Dotting NPH	.422	.643		.68
Coin Rotation NPH			.903	.88
Coin Rotation PH			.831	.78
Peg Board NPH	.410		.743	.74

Table 5. Pearson correlations calculating split half reliabilities of odd and even epochs, firstly across each motor-task and for both hands (for experiment 2), and secondly for the word generation speech task for experiment 1 and experiment 2. The mean number of trials accepted for each task is also included. * *denotes significant correlation*

	Left Hand			**Right Hand**		
	Mean accepted trials (total = 15)	*r*	*p*	Mean accepted trials (total = 15)	*r*	*p*
Pegboard	13	.54	.02*	12	.55	.019*
Coin Rotation	14	.77	.001*	14	.55	.021*
Finger Tapping	11	.47	.05*	13	.51	.03*
	Experiment 1			**Experiment 2**		
	Mean accepted trials (total = 23)	*r*	*p*	Mean accepted trials (total = 23)	*r*	*p*
Word Generation	21	.62	.001*	21	.68	.001*

Table 6. One sample T-tests to assess whether LI scores for the motor and speech tasks are significantly different to zero, for experiment 2. Significant results indicate that LI scores show lateralised hemispheric activation (either to the left- or right- hemisphere), and non-significant scores indicate a bilateral hemispheric activation pattern. **denotes significance*

	Left Hand				**Right Hand**			
	Mean	*SD*	*t*	*p*	Mean	*SD*	*t*	*p*
Pegboard	-.44	1.29	-1.55	.14	1.69	1.3	5.96	.001*
Coin Rotation	-1.69	1.1	-7.29	.001*	.57	1.4	1.88	.07
Finger Tapping	-2.1	1.14	-8.41	.001*	1.19	1.3	4.41	.001*
Word Generation	2.03	1.87	5.09	.001*	2.03	1.87	5.09	.001*

Table 7. Summary of multiple regression analysis for the motor-skill variables predicting speech lateralisation indices.

		B	***SE B***	**β**	**p**
Model 1	Constant	3.16	0.64		.001
	Pegboard – Right Hand	0.66	0.3	-.45	.042

Note: Model 1; $R^2 = .22$ (*ps* < 0.05); excluded variables = Pegboard (Left-hand); Coin (Left-hand); Coin (Right-hand); Finger Tapping (Lefthhand); Finger Tapping (Right-hand).

Table 8. Pearson R values for the LI scores from the three motor tasks, for right and left hands, and for the speech LI scores from Experiment 2. * indicates p < 0.05;

	Motor Task	**Speech LI score**
Right Hand (Mean LIs)	Pegboard	-.45*
	Coin Rotation	.05
	Finger Tapping	-.17
Left Hand (Mean LIs)	Pegboard	-.29
	Coin Rotation	-.05
	Finger Tapping	.41

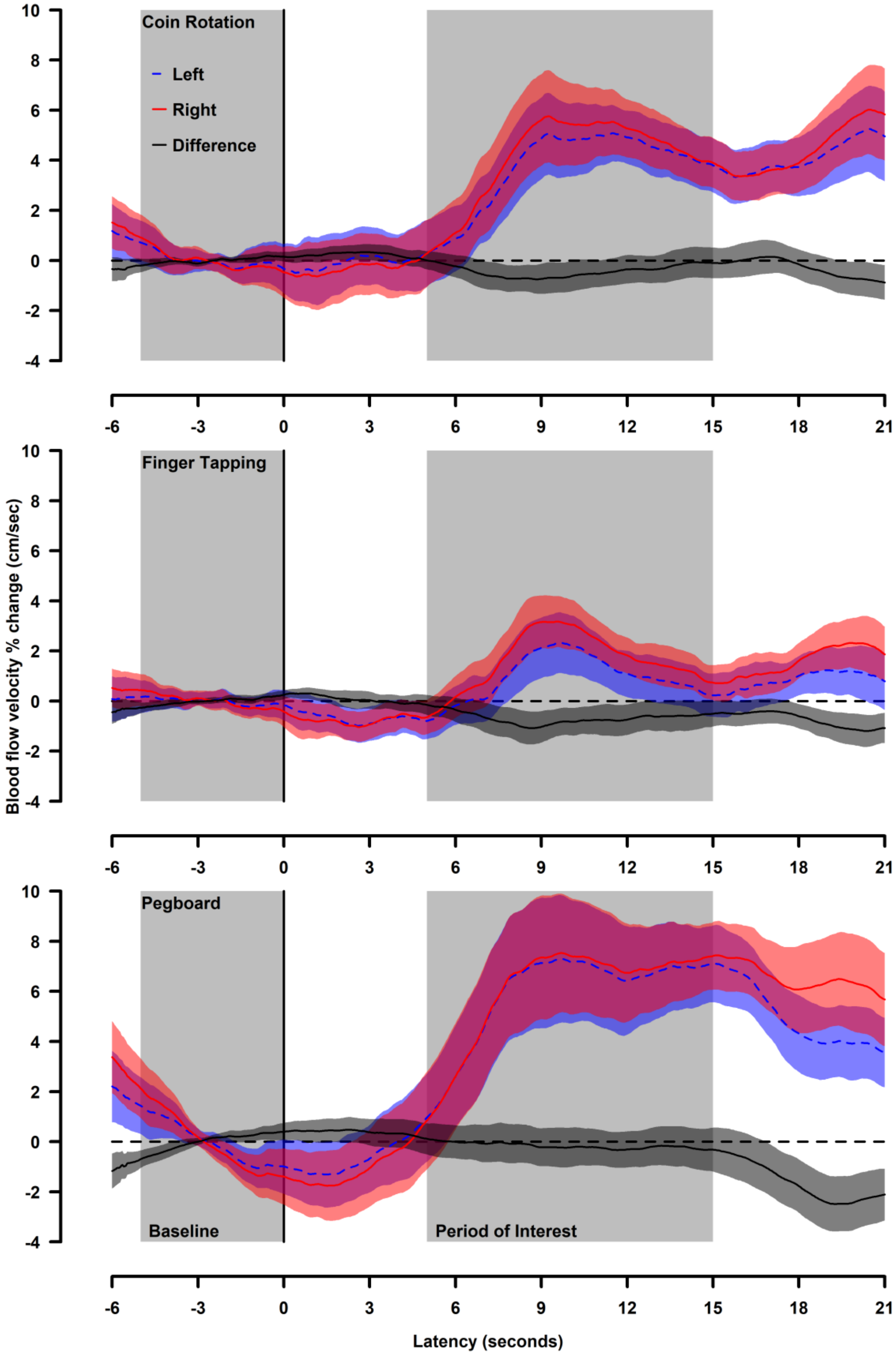
Coin Rotation
Left
Right
Difference
Finger Tapping
Pegboard
Baseline
Period of Interest
Blood flow velocity % change (cm/sec)
Latency (seconds)
10
8
6
4
2
0
-2
-4
-6
-3
0
3
6
9
12
15
18
21

Figure 1. fTCD evoked flow plots for each task showing the left- and right-hemisphere signals, and the difference between the left and right, over the time course of an epoch. Error bars represent 95% confidence intervals.

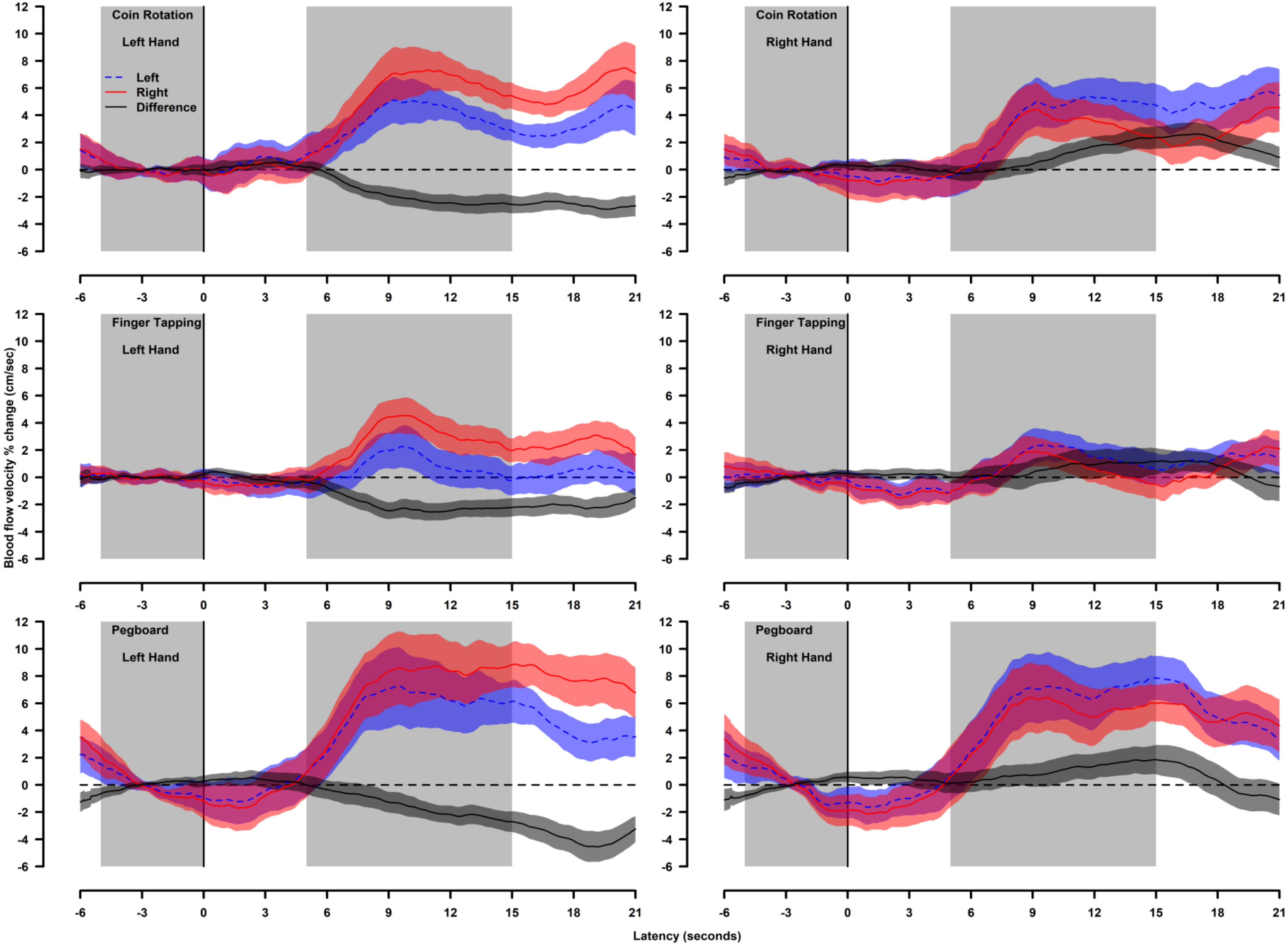
Coin Rotation
Left Hand
Left
Right
Difference
Coin Rotation
Right Hand
Finger Tapping
Left Hand
Finger Tapping
Right Hand
Pegboard
Left Hand
Pegboard
Right Hand
Blood flow velocity % change (cm/sec)
Latency (seconds)
12
10
8
6
4
2
0
-2
-4
-6
-6
-3
0
3
6
9
12
15
18
21

Figure 2. fTCD evoked flow plots for each task and each hand. Each plot shows the left (blue) and right (red) hemispheric activation patterns across time, with the difference between the left and right denoted in black. Error bars represent 95% confidence intervals.

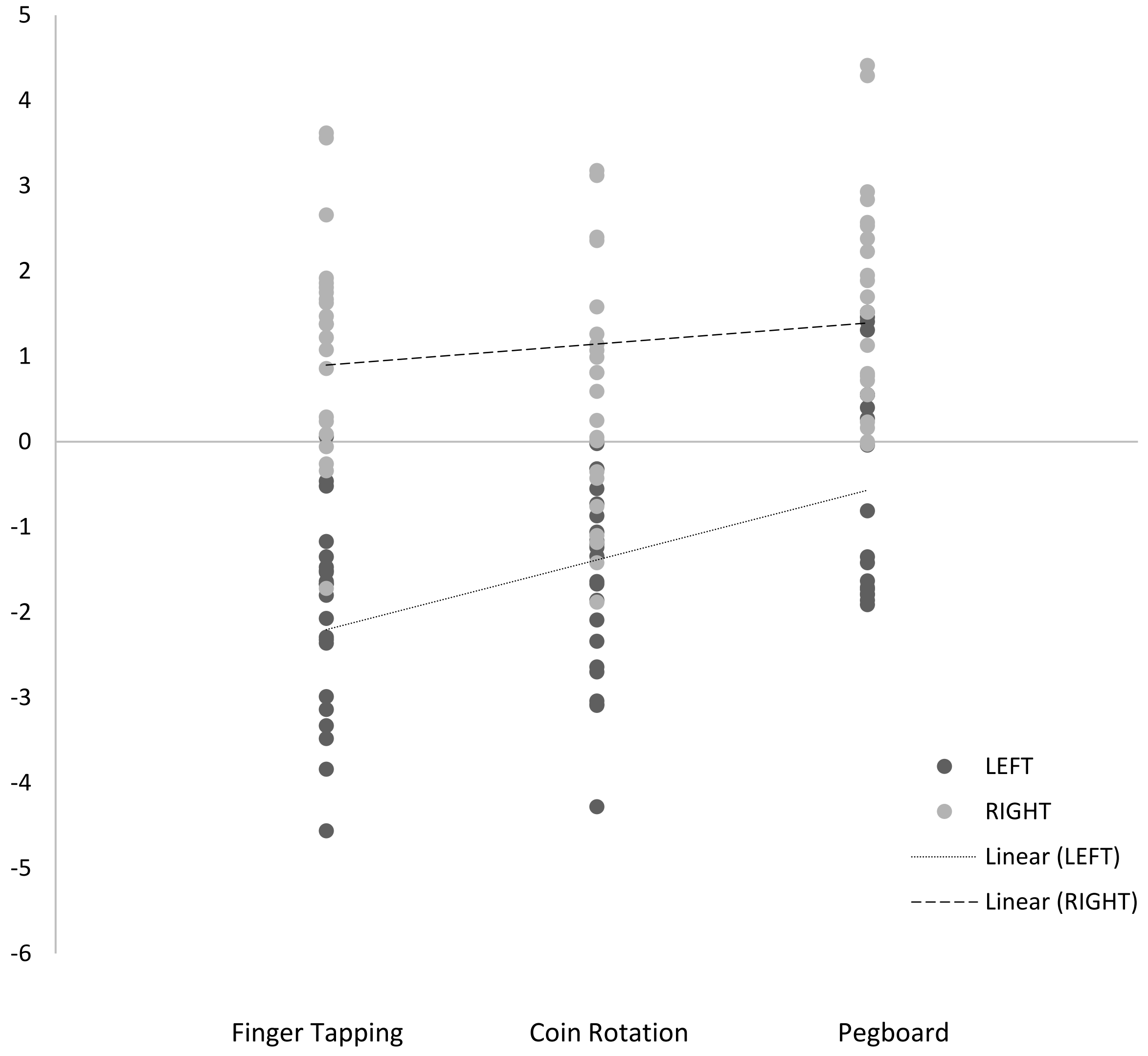

Figure 3. Plot showing mean hemispheric lateralisation index values produced by the movement of each hand, across each task. Negative values indicate right-hemisphere activation and positive values are left-hemisphere activation. Linear regression lines are fitted for the left- and right-hands.

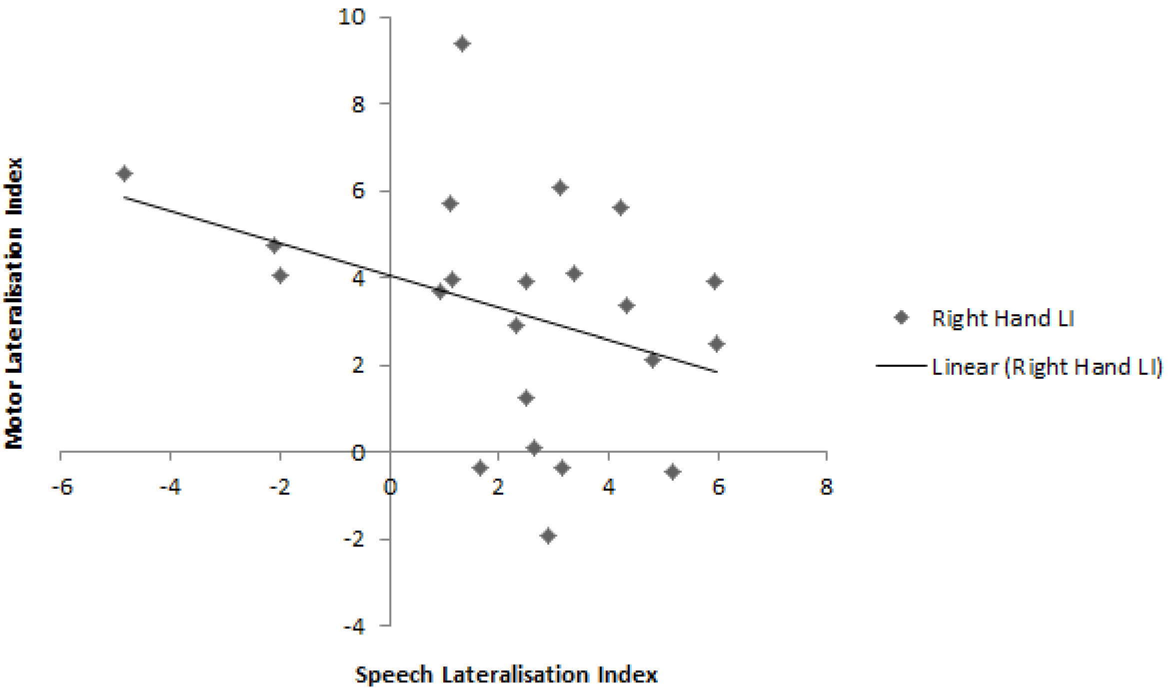

Figure 4. (Right-hand movement vs speech) Plot showing the mean lateralisation index scores for the word generation task compared to the motor lateralisation indices derived from the pegboard task, for the **right-hand**. Positive values indicate left-hemisphere activation; negative values indicate right-hemisphere activation.

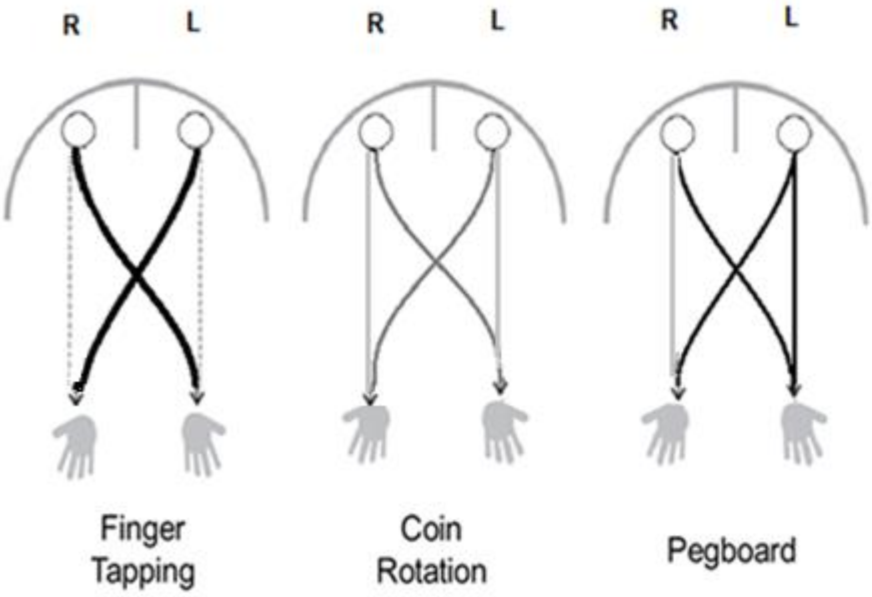

Figure 5. Schematic representing the activation patterns derived from the fTCD motor paradigm. Shading of the line relates to strength of activation. Dotted line indicates weak, but discernible activation.