Manual dexterity: functional lateralisation patterns and motor efficiency

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Abstract

Manual tasks are an important goal-directed ability. In this EEG work, we studied how handedness affects the hemispheric lateralisation patterns during performance of visually-driven movements with either hand. The neural correlates were assessed by means of EEG coherence whereas behavioural output was measured by motor error. The EEG data indicated that left- and right-handers showed distinct recruitment patterns. These involved local interactions between brain regions as well as more widespread associations between brain systems. Despite these differences, brain-behaviour correlations highlighted that motor efficiency depended on left-sided brain regions across groups. These results suggest that skilled hand motor control relies on different neural patterns as a function of handedness whereas behavioural efficiency is linked with the left hemisphere. In conclusion, the present findings add to our understanding about principles of lateralised organisation as a function of handedness.

Key words: motor control, handedness, EEG, functional connectivity.

1. Introduction

Hemispheric asymmetries are a fundamental principle of brain organisation, impacting on neural processing and efficiency (Toga & Thompson, 2003). It is generally assumed that these evolved in human evolution with the emergence of higher-order cognitive and behavioural functions (Hughdahl, 2011). Hemispheric asymmetries not only link with functional specialisation of both sides of the brain but also with information exchange between the hemispheres, a role that is mainly provided by the corpus callosum (Ringo, Doty, Demeter, & Simard, 1994). This premise suggests that increased intrahemispheric specialisation associates with reduced interhemispheric communication. That is, bilateral (symmetric) circuitry relies more on exchange of information across hemispheres whereas unilateral (asymmetric) circuitry depends strongly on intrahemispheric processing. In this respect, the specialisation of the left hemisphere for motor control is a specific example of asymmetry in the functional layout of the brain. The left-sided dominance of the motor circuitry, concentrated around prefrontal, premotor, primary motor and parietal areas, has found confirmation in brain imaging work (Schluter, Krams, Rushworth, & Passingham, 2001; Serrien, Cassidy, & Brown, 2003) as well as in clinical studies that have shown that left hemisphere lesions cause more deficits in the control of either hand whereas right hemisphere lesions primarily evoke motor deficits of the contralateral hand (Wyke, 1971). However, hemispheric lateralisation reflects a relative rather than absolute dominance of the left hemisphere for motor control (Serrien, Ivry, & Swinnen, 2006). This implies that the right hemisphere has a role in movement control, with a distinct contribution to motor responses such that information communication across hemispheres is relevant to support the task demands. Furthermore, changes in information processing may be triggered by factors such as the task requirements (Gerloff, Corwell, Chen, Hallett, & Cohen, 1998), learning (Andres et al., 1999) and hand preference (Serrien, Sovijärvi-Spapé, & Farnsworth, 2012).

In previous work, the dominance of the left hemisphere for motor control has especially been documented for right-handers (Jäncke et al., 1998; Spapé and Serrien, 2010) for which structural as well as functional distinctiveness is observed in the left hemisphere (Amunts er al., 1996; Haaland, Harrington, & Knight, 2000). In contrast to findings from right-handers, fewer insights exist for left-handers. Overall, left-handers show a mirror-opposite and reduced hemispheric lateralisation as indicated from reduced structural asymmetries of the motor system

(Amunts et al., 1996) and less robust functional patterns for complex unimanual and bimanual movements (Kloppel et al., 2007; Serrien et al., 2012; Solodkin, Hlustik, Noll, & Small, 2001; Vingerhoets et al., 2012). Further evidence for movement-related differences between left- and right-handers is provided by research that has examined visuo-spatial adaptations (Begliomini, Nelini, Caria, Grodd, & Castiello, 2008; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Vingerhoets et al., 2012), and response parameterisation (Reid & Serrien, 2012; Solodkin et al., 2001; Vicario, Bonni, & Koch, 2011). Combined, these observations denote that the processing mechanisms for motor behaviour vary as a function of handedness. One specific research question with respect to handedness is whether the asymmetrical lateralisation of the motor circuitry as observed in right-handers enhances behavioural performance in comparison to left-handers who show a more symmetrical regulation of motor pathways. This evaluation would give an indication about hemispheric functionality and behavioural (dis)advantages of particular lateralisation patterns.

Despite progress in brain asymmetry research, the nature of functional differences between left- and right-handers is not fully understood. In this study, we contrast left- and right-handers during performance of a skilled unimanual task and sought to determine how variations in neural asymmetries relate to motor efficiency. More specifically, we address in this research whether distinct lateralisation as observed in left- vs. right-handers modulate the processing mechanisms that regulate behavioural efficiency. To this end, the data analysis focuses on electroencephalogram (EEG) coherence, which expresses functional interactions between brain regions (Gerloff et al., 1998; Serrien et al., 2003). Characterisation of functional connectivity patterns within and between hemispheres alongside measurement of motor output will provide increased insights into the contribution of both hemispheres for the control of unimanual movements and subsequent effects on behaviour in different population groups.

2. Method

2.1. Participants

Thirteen left-handers (age: 21.8±3.3 years, laterality index: -88.1±16.2) and thirteen right-handers (age: 21.5±2.9 years, laterality index: 79.9±13.4) participated in the research study.

Participants had no history of neurological or psychiatric illnesses as evaluated by a standardised questionnaire. Participants provided written informed consent prior to the experiment in accordance with the declaration of Helsinki. The study was approved by the ethics committee of the School of Psychology, University of Nottingham.

2.2. Task and procedure

Participants performed a visuomotor tracking task by turning the wheel of a control device (Hercules DJ mp3-e2) connected to a PC, which also showed visual stimuli on the display screen. Each trial started with symbols to indicate the type of trial. After 2.0±0.5 s, a fixation cross was present for 1 s. Thereafter, a target and tracking object appeared. The target object moved according to a speed level controlled by a double sinusoidal function. After 15 s, target and tracking object disappeared, followed by an inter-trial interval of 0.75±0.25 s. The task conditions included left and right hand movements, according to an easy and complex condition as a result of modifications to the sensitivity of wheel turning. Trials were presented in sets of 8 blocks during which the task conditions were randomized between blocks. During rest trials, participants would observe the target object. Participants received training trials before the start of the experiment. Short breaks were provided.

2.3. EEG recordings and measurements

EEG data were recorded using an Electrical Geodesic Inc. 128-channel system. The signal was amplified, sampled at 250 Hz, band-pass filtered (0.05-100 Hz) and vertex referenced. The BESA software (MEGIS Software GmbH, Gräfelfing, Germany) was used for data processing and included notch-filtering (50 Hz), band-pass filtering (1-60 Hz), and a virtual reference-free montage. Artifacts including eye movements and EMG-related activity were corrected with the pattern recognition tool. EEG coherence was calculated by means of complex demodulation (Hoechstetter et al., 2004) with a time-frequency resolution of 25 ms/2 Hz, and was used as a measure of functional connectivity

We used a region of interest approach based on earlier work and focused on a set of electrodes (Serrien et al., 2012) which permitted to establish functional connectivity patterns of interest (FOI) that addressed local interactions between brain regions. This resulted in intrahemispheric connectivity associated with the left side (F3-FC3, F3-C3, F3-P3, FC3-C3, FC3-P3, C3-P3) and right side (F4-FC4, F4-C4, F4-P4, FC4-C4, FC4-P4, C4-P4), whereas interhemispheric connectivity delineated couplings across hemispheres (F3-F4, FC3-FC4, C3-C4, P3-P4), and midline connectivity was labelled as an average across the Fz, Cz surface (overlaying supplementary motor area, SMA). F3/4, FC3/4, C3/4, and P3/4 were included to characterise the activity from the dorsal lateral prefrontal, premotor, primary sensorimotor, and superior parietal areas, respectively. The intrahemispheric, midline and interhemispheric connectivity circuits were subsequently labelled as brain systems of interest (BOI) in order to address widespread interactions. Coherence was estimated in the beta frequency band (14-28 Hz) due to its significance for motor behaviour (Gerloff et al., 1998; Serrien et al., 2003). Before statistical testing, coherence values were normalised by applying the inverse hyperbolic tangent. EEG power was assessed in the beta range at the individual electrodes and stabilized using a logarithmic transformation.

2.4. EEG and behavioural data analysis

Intrahemispheric coherence of left vs. right side was calculated with a ratio=1 expressing equal contribution of both hemispheres. For the interhemispheric and midline connections, the control (rest) conditions were used as a baseline for the calculations. The coherence data were analyzed by means of 2 x 2 x 2 ANOVAs with Handedness Group (left- vs. right-handers), Performing Hand (left vs. right) and Performance Condition (easy vs. complex).

The behavioural error defined as the root mean square error was calculated as the nearest distance between the tracking and target path, and used as a measure of motor efficiency. It was analyzed by means of 2 x 2 x 2 ANOVAs with factors: Handedness Group, Performing Hand and Performance Condition. In order to evaluate brain-behavioural associations, we further estimated Pearson correlation coefficients between the coherences of the individual FOI and motor error scores. This evaluation provides insights into the functional couplings that are crucial for optimal performance.

Pearson's correlation coefficients were further calculated: (1) between the averaged coherences of the BOI in order to establish widespread dependencies in functional organisation,

(2) between the coherence and power scores of the individual electrodes for assessing whether changes in power could have contributed to the modulations in coherence.

Bonferroni corrections were made for multiple comparisons where appropriate. Mean±SE scores are reported.

3. Results

3.1. Behavioural data

The ANOVA of motor error showed a significant main effect of Performance Condition, $F(1,24)=9.03$, $p<0.01$. The mean scores were 6.41±0.19, 7.10±0.21 for easy and complex trials, respectively. There was a significant Handedness Group x Performing Hand interaction $F(1,24)=6.07$, $p<0.05$. This interaction indicated no hand differences for left-handers ($p>0.05$) whereas right-handers demonstrated higher motor error when moving the left as compared to right hand ($p<0.05$). The mean scores for the left and right hand were 6.43±0.16 and 6.84±0.20 for left-handers, 7.25±0.23 and 6.50±0.22 for right-handers.

3.2. EEG data

Intrahemispheric connectivity: The ANOVA of the left-right hemisphere coherence ratio revealed a significant main effect of Handedness Group, $F(1,24)=4.60$, $p<0.05$, with right-handers (1.251±0.020) showing higher coherence than left-handers (1.043±0.018). There was a significant Handedness Group x Performing Hand interaction, $F(1,24)=5.37$, $p<0.03$ (Fig. 1, left panel). This interaction revealed similar left-sided dominance across hands for right-handers ($p>0.05$) whereas left hemisphere involvement increased for left-handers when moving the right as compared to left hand ($p<0.05$).

Insert Fig. 1 about here

Brain-behaviour correlation analysis demonstrated significant associations between intrahemispheric connectivity and motor error ($p<0.05$). Table 1 highlights the key involvement of left-sided regions in supporting motor efficiency, with premotor cortex taking a prime role across handedness groups.

Insert Table 1 about here

Midline connectivity: The ANOVA of midline coherence demonstrated a significant main effect of Handedness Group, $F(1,24)=4.35$, $p<0.05$, with right-handers (1.142±.015) obtaining higher coherence as compared to rest than left-handers (1.054±0.014). The Handedness Group x Performing Hand interaction was significant, $F(1,24)=4.43$, $p<0.05$ (Fig. 1, right panel). This interaction revealed no hand differences for left-handers ($p>0.05$) whereas right-handers showed higher coherence when moving the left as compared to right hand ($p<0.05$).

Brain-behaviour correlation analysis identified no significant associations between midline area and motor error ($p>0.05$).

Interhemispheric connectivity: The ANOVA of interhemispheric coherence demonstrated a significant main effect of Handedness Group, $F(1,24)=5.91$, $p<0.03$, indicating distinct information processing between hemispheres during movement as compared to rest in left-handers (1.066±0.013) vs. right-handers (0.891±0.016). There was a significant main effect of Performance Condition, $F(1,24)= 6.45$, $p<0.02$, with reduced coherence in easy as compared to complex trials. The mean scores were 0.965±0.012 and 1.127±0.015, respectively.

Brain-behaviour correlation analysis showed no significant correlations between the interhemispheric connections and motor error ($p>0.05$).

BOI: Correlation analysis between the intrahemispheric, midline and interhemispheric systems demonstrated significant associations for complex movements, hinting at defined links between circuitry with distinct processing roles. This system-based processing was observed to be similar across handedness groups for right hand movements, with an inverse relationship between intra- and interhemispheric connectivity ($r=-0.58$ for left-handers and $r=-0.55$ for right-handers). Conversely, for left hand movements, a negative correlation was noted between midline and interhemispheric connectivity for right-handers only ($r=-0.70$).

Coherence-power analyses: correlations between the coherence scores of the couplings and the power scores of the individual electrodes revealed no significant effects, $p>0.05$. This suggests that coherence changes were independent of power modulations.

4. Discussion

The present research evaluated the cortical dynamics of unimanual movements. In particular, we studied the functional connectivity patterns between key regions of the motor circuitry, based on the premise that these profiles provide insights into the way that brain sites work together for implementing higher-order functions (Uhlhaus & Singer, 2006). That is, we assessed the relative strength of the neural connections and examined how these linked with behavioural performance as a function of handedness. It was argued that an analysis of the functional brain asymmetries alongside the motor output would be important to reveal changes in the neural organisation mechanisms that characterise left- and right-handers.

4.1. Functional connectivity patterns

In previous studies, EEG coherence has been used as an index of brain connectivity that describes functional coordination patterns during perceptual, cognitive and motor processes (Knyazeva, Fornari, Meuli, Innocenti, & Maeder, 2006; Serrien 2008; Thomas, Dalecki, & Abeln, 2013). Here, we observed that unimanual movements modulated functional connectivity within and across hemispheres as a function of handedness. For intrahemispheric connectivity, right-handers showed consistent enhanced coherence in the left as compared to right hemisphere, independent of hand moved. This observation underlines a tight left-sided lateralisation in right-handers. Conversely, left-handers demonstrated a more dynamic pattern with adaptation as a function of hand moved. This finding indicates flexibility of the coupling mechanisms that underlie the functional organisation of manual actions, which can partly be due to the experience that left-handers have in using both hands, influencing their motor repertoire.

We also noted that midline connectivity (involving SMA) played a selective mediating role for supporting movements in right-handers. In particular, right-handers showed higher coherence for left than right hand movements, which is likely due to the increased task complexity when right-handers move their non-dominant hand. These adaptations are in line with a role of the

SMA for the organisation of hand movements (Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000) as well as performance monitoring and error processing (Bonini et al., 2014).

Interhemispheric connectivity was higher in left- than right-handers. This observation supports data that have revealed that interactions between hemispheres underline changes in processing demands due to handedness (Pool, Rehme, Fink, Eickhoff, & Grefkes, 2014; Reid & Serrien, 2012). Here, we noticed that right-handers showed suppression during movement as compared to rest, which suggests that inhibition of the contralateral hemisphere assists functional lateralisation. In particular, strong interhemispheric inhibition during movement organisation would support unwanted crosstalk between hemispheres.

Combined, the present data demonstrate that unimanual movements are driven by flexible interactions between brain sites. Furthermore, left- and right-handers showed distinct functional organisation profiles for intrahemispheric, midline and interhemispheric circuits, suggesting that closely related motor tasks can rely on different cortical processing mechanisms. Flexible regulation is particularly important for higher-order functions such as action planning, which require a high degree of information integration from different brain sources (Uhlhaas and Singer, 2006). It further underlines the asymmetrical involvement of the hemispheres in motor control, and suggests that various pathways are involved in the formation of lateralised higher-order functions.

4.2. Brain-behaviour and brain system correlations

Brain-behaviour correlation analyses were conducted as they relate the outcome of information processing with the neural correlates that underlie the processes. The present data showed that increases in neural coupling predicted optimal task performance such that stronger functional connectivity associated with smaller motor error. In this respect, brain regions localised within the left hemisphere, dorsolateral prefrontal (PFC), premotor (PMC) and primary motor cortex (M1), were vital for an efficient motor output. These are key regions that promote motor behaviour, with PMC figuring as a central site that operated across handedness groups. Whereas dorsolateral PFC plays a crucial role in the formation of the response output (Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006), PMC is crucial for the organisation of externally triggered actions that rely on visuomotor transformations (Debaere, Wenderoth, Sunaert, Van

Hecke, & Swinnen, 2004; Halsband, Ito, Tanji, & Freund, 1993) and M1 subserves the final control requirements. Combined, the findings underline the significance of left-sided brain areas in supporting a system that guides the efficient organisation of motor outcomes. In particular, the data showed a direct association between neural connectivity strength of prefrontal-premotor-primary motor areas and successful behavioural performance. However, although PMC played a central role in supporting motor efficiency, its connections with the other left-sided brain areas was not fixed. That is, whereas the coupling with PFC was prominent across handedness group, the connection with M1 was crucial for right-handers only. This finding suggests an increased reliance of the left-sided M1 for supporting behavioural output in right-handers. It is noteworthy to add that although differences in attentional regulation are observed in left- as compared to right-handers (Buckingham, Main, & Carey, 2011), the discrepancy in types of functional interactions we noted between left- and right-handers can be argued to reflect modulations in motor regulation. In particular, handedness distinctively shapes the functional connectivity patterns between left-sided PFC, PMC and MI, which selectively impacts on behavioural efficiency.

The BOI correlation analyses specified that the coordination of brain systems (i.e., intrahemispheric, interhemispheric and midline circuitry) guided movement organisation in left- and right-handers as a function of task complexity. In particular, negative correlations were noted between intra- and interhemispheric connectivity for both handedness groups when moving their right hand. This indicates that an inverse relationship exists between these brain systems in situations when the left hemisphere dominates the processing demands for guiding right hand performance. A further negative correlation was observed for right-handers between interhemispheric and midline connectivity when they moved their left hand. Therefore, midline circuitry represents a relevant pathway that supports functional coupling patterns when right-handers perform movements with the non-dominant hand. This observation is in line with earlier fMRI research that has revealed that handedness guides effective connectivity within the motor network, including a significant role of the SMA (Pool et al., 2014). Taking into account that the coordination of brain systems was observed for complex rather than easy movements without a behavioural handedness effect, it suggests that these widespread interactions have limited influence in supporting behavioural efficiency as compared to localised interactions between left-sided brain regions.

In conclusion, the data underline that left- and right-handers recruit distinct neural dynamics when performing unimanual movements. This concerns local interactions between brain regions as well as more widespread associations between brain systems. Despite these differences, brain areas within the left hemisphere were crucial for implementing behavioural efficiency across handedness groups. These results add to insights about brain organisation for hand motor control as a function of handedness.

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Figure caption

Fig. 1. Intrahemispheric (left panel) and midline (right panel) connectivity scores, illustrating group differences as a function of hand moved. Means and SEs are shown.

Table caption

Table 1. Correlation scores between the coherence of left-sided brain regions and motor errors for easy and complex movements in left- and right-handers.

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