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Research report

Hemispheric asymmetries and the control of motor sequences

Deborah J. Serrien *, Michiel M. Sovijärvi-Spapé

School of Psychology, University of Nottingham, University Park, Nottingham, NG7 2RD, UK

HIGHLIGHTS

- The EEG study examines unimanual and bimanual sequencing in left- vs. right-handers.
- Superiority of higher-order action processing in the left hemisphere.
- The lateralisation profile is independent of hand dominance and task demands.

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ABSTRACT

Sequencing of finger positions reflects a prototype of skilled behaviour. In order to perform sequencing, cognitive control supports the requirements and postural transitions. In this electroencephalography (EEG) study, we evaluate the effects of hand dominance and assess the neural correlates of unimanual and bimanual sequencing in left- and right-handers. The behavioural measurements provided an index of response planning (response time to first key press) and response execution (time between successive key presses, taps/s and percentage of correct responses), whereas the neural dynamics was determined by means of EEG coherence, expressing the functional connectivity between brain areas. Correlations between brain activity and behaviour were calculated for exploring the neural correlates that are functionally relevant for sequencing. Brain–behavioural correlations during response planning and execution revealed the significance of circuitry in the left hemisphere, underlining its significant role in the organisation of goal-directed behaviour. This lateralisation profile was independent of intrinsic constraints (hand dominance) and extrinsic demands (task requirements), suggesting essential higher-order computations in the left hemisphere. Overall, the observations highlight that the left hemisphere is specialised for sequential motor organisation in left- and right-handers, suggesting an endogenous hemispheric asymmetry for compound actions and the representation of skill; processes that can be separated from those that are involved in hand dominance.

1. Introduction

Sequencing of finger positions reflects a prototype of skilled behaviour. This type of activity not only involves motor regulation that integrates the timing demands but also higher-order organisation that enables the transitions between the different fingers. In right-handers, sequencing with either hand strongly relies on the integrity of the left hemisphere and in particular on the premotor and parietal areas [16,28], which suggests the significance of the left hemisphere for motor acts. The latter is also supported from patient studies that have revealed that motor skills are disrupted by lesions of the left hemisphere even when the ipsilesional hand performs, whereas damage of the right hemisphere only produces minor deficits on the ipsilateral side [14]. Furthermore, patient data have shown that left hemisphere lesions have a stronger impact on the performance of intricate heterogeneous as compared to simple repetitive sequences, which suggests that compound responses strongly rely on the left hemisphere [16]. Combined, the existing research work indicates the importance of resources localised in the left hemisphere for heterogeneous sequential responses.

In the area of motor control, hemispheric dominance is a highly debated topic [46] and especially relevant in relation to handedness. In this respect, the neural correlates of skilled actions have particularly been examined in right-handers. Conversely, the neural dynamics of left-handers has received less consideration. Overall, it has been suggested that both handedness groups have dissimilar activation patterns with left-handers demonstrating less hemispheric asymmetries than right-handers when performing complex unimanual and bimanual tasks [25,35,50,56]. These differences in neural asymmetries may further relate with changes

* Corresponding author. Tel.: +44 115 951 5285; fax: +44 115 951 5324.
E-mail address: Deborah.Serrien@nottingham.ac.uk (D.J. Serrien).

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in information processing that effect on behavioural performance [3,6,23,55] and that especially become prominent as a function of task complexity [50]. Building on previous research work, the aim of the present electroencephalogram (EEG) study is to evaluate the neural correlates of unimanual and bimanual sequencing in left- vs. right-handers. Data analysis focuses on EEG coherence, which provides an index of interregional information processing and functional connectivity, based on the premise that synchronised neural activity represents a means to realise dynamic interactions between widespread brain areas for supporting task performance [11,53]. In this respect, the importance of functional connectivity measures is particularly provided by research work that has demonstrated associations between the degree of functional coupling and the efficiency of behavioural output [20,29]. In the present context, we assess the functional significance of hemispheric connectivity patterns for the planning and execution of motor sequences. The hypothesis was made that left- and right-handers would show distinct interregional connectivity profiles for unimanual and bimanual performance conditions due to differences in control mechanisms and hemispheric asymmetries that distinguish both handedness groups.

2. Materials and methods

2.1. Participants

Thirteen left-handed (three male, ten female, age: 23.5 ± 4.9 years; age range = 18–34 years) and 13 right-handed participants (four male, nine female, age: 21.2 ± 2.2 years; age range = 18–27 years) took part in the experiment. Their mean laterality index determined by the Edinburgh handedness inventory was -89.1 ± 3.1 for the left-handers and 88.4 ± 11.9 for the right-handers [31]. The study was approved by the ethics committee of the School of Psychology, and all participants gave informed written consent to participate in accordance with the declaration of Helsinki.

2.2. Task and procedure

Prior to the EEG experiment, participants completed behavioural performance tasks: (1) a tapping task (by pressing the spacebar of a keyboard for 10 s with the left and right index), (2) the Purdue pegboard task (by placing pegs) with the left, right and both hands. There were three trials for each performance condition and the different assignments were counterbalanced across the participants. The tapping and pegboard tasks were included in the study as they are often used to measure manual proficiency in terms of motor speed and dexterity [9,52].

The EEG experiment required participants to perform a memory-guided sequencing task with one or both hands using RB-830 response box (Cedrus, San Pedro, CA). The key presses were made with the index, middle and ring fingers, which were associated with the respective numbers 1, 2 and 3. In each trial, a baseline interval (500 ms) was followed by a cue that indicated the hand(s) with which the sequence was to be performed; i.e., left (<), right (>) or both (<, >). Thereafter, a 5-digit number was displayed on the computer screen that represented a sequence of key presses consisting of four finger transitions (e.g., 21323) and that required memorisation. After 3.5 ± 0.5 s, the 5-digit number was replaced by a black fixation cross for 0.75 ± 0.25 s. Then, a go cue (green fixation cross) appeared, prompting the participants to execute the prepared sequence as quickly and accurately as possible without visual guidance. Participants were required to repeat the sequence until the green fixation cross coloured red 5 s later. In the bimanual condition, the hands executed mirror-symmetric sequences. Training trials were included during which participants received feedback about their performance. A total of 192 trials was performed and the different hand conditions were counterbalanced. The sequences used in the experimental design consisted of different orderings of finger movements across trials and had matched difficulty, based on pilot experimentation in which we also examined the response times of the individual key presses. The results revealed that the participants organised the responses as a single motor chunk. Indicative of a motor chunk is a relatively slow initiation (i.e., first key press) followed by faster subsequent responses. There was no evidence of multiple motor chunks, i.e., key presses with a long response time after the first one, which would point to additional preparation processes [54].

2.3. Recordings and measurements

In the tapping and pegboard tasks, the number of taps and pegs were measured. Average scores for the three trials per task condition were calculated. In the sequencing tasks, the measurements comprised the response time between go signal and first key press of the sequence (first RT) as an indication of response planning, in addition to the time between successive key presses (IRI), number of key presses in 5 s (taps/s) and percentage of correct responses (response accuracy) as an estimate of response execution. Trials with one or more incorrect finger presses were not included in the temporal analyses.

Continuous EEG was 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. Data pre-processing was carried out using BESA software (MEGIS Software GmbH, Gräfelfing, Germany), including notch-filtering at 50 Hz, band-pass filtering (1–60 Hz), and re-referencing to a virtual reference free montage. Artefacts such as eye movements and EMG-related activity were corrected with a pattern recognition algorithm as integrated within the BESA software. The intervals that represented planning and execution of the sequences were segmented into epochs of 300 ms with 128 ms of overlap. This resulted in an average of 506 ± 94 segments for the response planning interval and 651 ± 132 segments for the response execution interval, per participant and per performance condition.

EEG coherence was used as an index of functional coupling. Coherence is a normalised measure that quantifies the linear relationship between two signals in the frequency domain and varies between 0 (no correlation) and 1 (perfect correlation). Coherence values were computed by means of complex demodulation as implemented in BESA [21], with a time-frequency resolution of 2 Hz/25 ms.

Coherence was calculated in the lower beta band (13–21 Hz) due to its significance for information processing in large-scale networks during motor tasks [48]. To assess indices of cortical activity, a region of interest approach was adopted, which focused on a restricted number of electrodes. This included the midline (Fz, FCz; labelled as midline, M), intrahemispheric left (F3, FC3, C3, P3), and intrahemispheric right (F4, FC4, C4, P4), with F3/4, FC3/4, C3/4, and P3/4 expected to overlie the dorsal prefrontal, premotor, primary sensorimotor, and superior parietal areas. The couplings were divided into intrahemispheric left (F3-FC3, F3-C3, F3-P3, FC3-C3, FC3-P3, C3-P3), intrahemispheric right (F4-FC4, F4-C4, F4-P4, FC4-C4, FC4-P4, C4-P4), interhemispheric (F3-F4, FC3-FC4, C3-C4, P3-P4), left-midline (F3-M, FC3-M, C3-M, P3-M), and right-midline (F4-M, FC4-M, C4-M, P4-M). Prior to statistical testing, a variance stabilising transform was used [17]. EEG power was calculated at the individual electrodes by means of the complex demodulation procedure, followed by a logarithmic variance