Functional Connectivity Patterns During Motor Behaviour: The Impact of Past on Present Activity

Deborah J. Serrien*

*School of Psychology, University of Nottingham, University Park,
Nottingham NG7 2RD, United Kingdom*

Abstract: Everyday behaviour often depends on the performance of multiple movements executed in a particular order. Here, the impact of task history on the neural activation patterns of motor behaviour is examined by evaluating unimanual and bimanual actions that are produced in a serial arrangement, such that switching between tasks is required. Cortical dynamics was assessed by means of EEG coherence in the β frequency band (13–30 Hz). Results showed that although behavioural performance was not affected, switching trials induced increased coherence as compared to control (repeat) trials. This reorganization was dependent on task history and was more pronounced for unimanual than for bimanual tasks. Overall, the data illustrate that neural processing of motor behaviour within a serial arrangement integrates past and present activity, and accordingly impacts on neural efficiency. *Hum Brain Mapp* 30:523–531, 2009. © 2007 Wiley-Liss, Inc.

Key words: EEG; coherence; functional connectivity; bimanual coordination; task switching

INTRODUCTION

Many everyday activities depend on the organization of motor tasks that require the performance of individual movements in a successive and sometimes variable order. For example, unlocking the door might follow from a preceding action when the key needs to be grasped from the table, is received from someone else, etc. This example illustrates that the means by which a particular task is performed relies on the context set by the task history. Accordingly, it can be argued that the preceding task requirements operate as a dynamic base-

line for a subsequently performed assignment. This issue becomes especially challenging when executing motor tasks that are known from organisational principles, to differ in processing demands such as those that implicate the performing hand or task complexity [Serrien et al., 2006]. In particular, a contralateral organization prevails for unimanual movements, whereas a left hemisphere dominance has been associated with bimanual movements [Jäncke et al., 1998; Serrien et al., 2003; Viviani et al., 1998; but see Chen et al., 2005; Foltys et al., 2001]. Taking into account these organizational principles, the premise can be made that the neural dynamics associated with a particular assignment within a serial arrangement will differ depending on the previous task requirements because of an imposed reorganisation of the existing activity.

The issue of multi-task regulation during which various assignments are performed subsequently has been examined in the literature from a task-switching perspective. This line of work has revealed that subjects react slower (and are more prone to errors) during switch than repeat trials [e.g., Allport et al., 1994; Meiran, 1996; Rogers and Monsell, 1995]. The presence of such switch costs implies

Contract grant sponsor: Research Committee (NRF) of the University of Nottingham.

*Correspondence to: Deborah Serrien, School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, United Kingdom. E-mail: deborah.serrien@nottingham.ac.uk

Received for publication 25 August 2007; Revised 21 October 2007; Accepted 27 October 2007

DOI: 10.1002/hbm.20518

Published online 19 December 2007 in Wiley InterScience (www.interscience.wiley.com).

that task selection of subsequent assignments is not optimal. In view of motor control, the switching paradigm has been used to study transitions between coordination modes and effector combinations. Commonly it is observed that coordinative stability determines switching time. In particular, switching is faster from a less stable to a more stable coordination pattern than vice versa [Kelso et al., 1988; Serrien and Swinnen, 1999]. Following up on this work, the present study assesses whether neural regulation of motor performance is influenced during switch as compared to control (repeat) trials. Various task combinations that make up a series of motor actions are included in the experimental design.

To evaluate the neural activation patterns, the data analysis in this study focuses on EEG coherence that expresses functional interactions between brain areas [e.g., Blum et al., 2007; Gerloff et al., 1998; Serrien and Brown, 2003]. The argument is put forward that task performance underlies distinctive information processing between the large-scale regions of the motor network, which depends on the performing hand and task complexity. Accordingly, executing a serial arrangement that is composed of different motor assignments will impose neural reorganization because of changes in the behavioral demands. In this respect, few details are known about the consequences that dynamic patterns of hemispheric activation have on subsequent processing, although previous trial effects have been reported [Fecteau and Munoz, 2003].

Here the hypothesis is made that neural activity associated with a motor task within a serial arrangement is shaped by the characteristics of the preceding task requirements. Because of this contextual constraint, task switching will cause higher demands on the motor system than repeat (no switching) conditions, resulting in increased neural effort. It is argued that an evaluation of interregional coupling patterns during switching conditions will provide detailed information concerning the impact of past on present activity. In this work, the focus is on delineating the connectivity patterns of the motor network that supports task performance; this will enable to extend previous observations concerning switch costs and the toll on efficiency when transitions between tasks arise.

METHODS

Participants and Tasks

Eight right-handed participants (age: 24 ± 4 years) as determined by the Edinburgh handedness inventory [Oldfield, 1971] gave informed consent to participate in the study, which was approved by the local ethics committee. They were asked to perform externally paced tapping movements on a keyboard. The metronome pace was set at a comfortable cycle duration of 500 ms. There were three different tasks: tapping with the right index, tapping with the left index, bimanual tapping with both indexes according to an in-phase (symmetrical) mode.

Subjects performed trials that included the performance of three successive motor tasks. These could be different from one another (e.g., segment 1 = right, segment 2 = left, segment 3 = bimanual) or repeated for a task (e.g., segment 1 = right, segment 2 = left, segment 3 = right). A variety of 12 task combinations was used (six combinations that involved three different tasks and six combinations that required two different tasks, thus containing the same task during segments 1 and 3). The combinations that involved three different tasks were (1) right, bimanual, left, (2) left, bimanual, right, (3) right, left, bimanual, (4) left, right, bimanual, (5) bimanual, right, left, (6) bimanual, left, right. The combinations that involved two different tasks were (7) right, left, right, (8) left, right, left, (9) bimanual, left, bimanual, (10) bimanual, right, bimanual, (11) right, bimanual, right, (12) left, bimanual, left. Trials lasted 2 min each, with a task shift being introduced after 40 s. Three control (repeat) combinations were also included and required the same motor task to be performed for the total duration of the trial (e.g., segment 1 = right, segment 2 = right, segment 3 = right). Two trials per task combination were performed. There were small breaks in between trials for avoiding fatigue and loss of attention. EEG activity was continuously recorded.

Subjects were told that a trial consisted of three tasks performed in a successive order. The behavioural requirements of the motor tasks for the segments 2 and 3 were instructed by means of a cue, so that the degree of anticipation was similar across all conditions to avoid specific proactive recruitment [Serrien et al., 2004]. Subjects were advised to make the task switch as smoothly as possible, without stressing reaction time. When performing a unimanual task, the switch implicated a change to an alternative unimanual condition (i.e., switching between hands) or to a bimanual condition, whereas for the bimanual task the switch involved a change to a unimanual condition.

EEG Recordings and Analysis

Continuous EEG was recorded using the Electrical Geodesics 128-channel system, and data processing was carried out using Brain Vision Analyzer software (Brain Products, München, Germany). EEG signals were amplified, band-pass filtered (0.01–100 Hz) and sampled at 250 Hz with a vertex reference. Re-referencing was conducted by estimating Hjorth derivations. Epochs contaminated by eye movements, blink and EMG-related activity were rejected after removal of slow drifts by linear trend correction and baseline correction.

EEG coherence was used to assess functional coupling between cortical areas in the frequency domain, and was estimated using the discrete Fourier transform and parameters derived from it. As a normalised measure of coupling between two signals at any given frequency, it varies between 0 (no correlation) and 1 (perfect correlation). Coherence $|R_{ab}(\lambda)|^2$ was calculated by using the formula: $|R_{ab}(\lambda)|^2 = |f_{ab}(\lambda)|^2 / f_{aa}(\lambda)f_{bb}(\lambda)$. In this equation, f char-

acterises the spectral estimate of two EEG signals a and b for a given frequency (λ). The numerator includes the cross-spectrum for a and b (f_{ab}), whereas the denominator includes the autospectra for a (f_{aa}) and b (f_{bb}). Coherence was estimated for the different trials and divided into segments of identical duration for each task. The first and last 3 s of each segment was eliminated to limit motion onset and offset transients. The analysis accordingly excluded the switching process that steered the transition from one motor task to the next.

To assess indices of cortical activity, a region of interest approach was adopted, which focused on a restricted number of electrodes. This division resulted in intrahemispheric and interhemispheric connections, based on earlier EEG-studies of unimanual and bimanual movement control [Hummel et al., 2002; Serrien and Brown, 2003] and included the following connectivity groupings: intrahemispheric left (FC3-C3, FC3-CP3, FC3-P3, C3-CP3, C3-P3, CP3-P3), intrahemispheric right (FC4-C4, FC4-CP4, FC4-P4, C4-CP4, C4-P4, CP4-P4) and interhemispheric (FC3-FC4, C3-C4, CP3-CP4, P3-P4). Coherences were evaluated in the β frequency band (13–30 Hz) because of its importance for motor behaviour [Gerloff et al., 1998; Serrien and Brown, 2003]. Before statistical operations were conducted, coherences were transformed using the inverse hyperbolic tangent to stabilise variances. In addition, EEG power was measured in the β band at the individual electrodes and stabilised by logarithmic transformation. Averages were estimated for the different conditions.

To examine the influence of task history on subsequent neural organization, the analyses focused on assessing the neural dynamics associated with a particular task, performed during the segments 2 and 3 of the serial arrangement. Control (repeat) conditions with no switching demands were also integrated in the analysis in order to contrast with the performance conditions when switching was required.

Behavioural Analysis

E-Prime software (Psychology Software Tools, Pittsburgh) was used to record the cycle durations from the key presses.

RESULTS

EEG Data: Coherence

Coherence was calculated across the motor network in order to obtain a measurement of overall neural activity. The network consisted of intrahemispheric and interhemispheric connectivity groupings. Mean $\pm$ SD scores are stated.

Segment 2

Control conditions. The control conditions of the different tasks during the segment 2 were contrasted in order to verify the neural dynamics under normal circumstances, i.e.,

Figure 1.

The performance conditions during segment 2 which include the task requirements of segment 1 for the different tasks; unimanual left (unimanual right = U_R, bimanual = B), unimanual right (unimanual left = U_L, bimanual = B), and bimanual (unimanual left = U_L, unimanual right = U_R). The control conditions of unimanual left (L), unimanual right (R) and bimanual (B) are also displayed. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

unaffected by switching performances. The analysis included a one-way ANOVA on task (unimanual left, unimanual right, bimanual) and revealed a significant effect [$F(2,14) = 5.9, P < 0.05$]. Post hoc analysis showed that the unimanual tasks did not differ from one another ($P > 0.05$), whereas both conditions showed lower coherence scores than the bimanual task ($P < 0.05$). The mean scores were 0.065 ± 0.021 , 0.068 ± 0.017 and 0.088 ± 0.020 for left, right and bimanual, respectively (Fig. 1, right-side panel).

Performance conditions. For the performance conditions, the segment 2 of the serial arrangement was analysed to examine effects of immediate task history (Fig. 1, left-side panel). For this purpose, the segment 2 was used of the combinations for which there were similar task requirements for the segments 1 and 3. This resulted in the evaluation of six conditions: right, left; bimanual, left; left, right; bimanual, right; right, bimanual; left, bimanual. In addition, the segment 2 of the control conditions was used. Various analyses were conducted as reported next.

Connectivity changes during switching conditions. The performance and control conditions of the different tasks were evaluated in order to assess the impact of task switching on the neural dynamics (see Fig. 1). The analyses involved one-way ANOVAs on condition that implicated the requirements of segment 1. They were conducted separately for the different tasks and resulted in the following analyses: unimanual left (unimanual right, bimanual and control), unimanual right (unimanual left,

bimanual and control) and bimanual (unimanual left, unimanual right and control).

Unimanual left: The analysis revealed a significant effect of segment 1 requirements [$F(2,24) = 25.9$, $P < 0.01$]. Post hoc analysis showed that all conditions differed from one another ($P < 0.05$). The mean scores were 0.094 ± 0.011 , 0.112 ± 0.017 and 0.065 ± 0.021 for unimanual right, bimanual and control, respectively.

Unimanual right: The analysis denoted a significant effect of segment 1 requirements [$F(2,24) = 65.5$, $P < 0.01$]. Post hoc analysis indicated that all conditions were different from one another ($P < 0.05$). The mean scores were 0.089 ± 0.021 , 0.114 ± 0.023 and 0.068 ± 0.017 for unimanual left, bimanual and control, respectively.

Bimanual: The analysis demonstrated a significant effect of segment 1 requirements [$F(2,24) = 4.9$, $P < 0.05$]. Post hoc analysis showed that both switching conditions differed from the control task ($P < 0.05$), whereas they did not differ from one another ($P > 0.05$). The mean scores were 0.110 ± 0.016 , 0.107 ± 0.015 and 0.088 ± 0.020 for unimanual left, unimanual right and control, respectively.

Intrahemispheric versus interhemispheric connectivity changes during switching conditions. Additional analyses were conducted that evaluated changes in connectivity within and between hemispheres. They were carried out separately for the combined unimanual tasks (because of their similarity in switching response) and bimanual task by means of 2×3 ANOVAs that implicated connectivity (intrahemispheric, interhemispheric) and condition (requirements during segment 1, which were unimanual, bimanual and control for the combined unimanual tasks; unimanual left, unimanual right and control for the bimanual task). For the unimanual tasks there was a main effect of connectivity [$F(1,7) = 11.4$, $P < 0.05$] and condition [$F(2,14) = 27.4$, $P < 0.01$]. The connectivity $\times$ condition interaction was also significant [$F(2,14) = 4.5$, $P < 0.05$]. Post hoc analysis showed that intrahemispheric and interhemispheric connectivity did not differ for the control task ($P > 0.05$), whereas interhemispheric connectivity was greater than intrahemispheric connectivity for the switching conditions ($P < 0.05$; see Fig. 2). The mean scores for intra- vs. interhemispheric connectivity were 0.075 ± 0.012 vs. 0.108 ± 0.020 (unimanual), 0.098 ± 0.018 vs. 0.128 ± 0.022 (bimanual) and 0.064 ± 0.016 vs. 0.070 ± 0.021 (control). For the bimanual task, a main effect of condition was observed [$F(2,14) = 4.4$, $P < 0.05$], highlighting the difference between switching and control conditions. No significant effect with respect to connectivity was observed ($P > 0.05$).

Comparing the different tasks during switching conditions. An additional analysis was conducted that contrasted the three different tasks. This analysis permitted to assess the impact of the performing hand as well as task complexity upon the post-switching neural dynamics. It involved a 3×2 ANOVA that integrated task (unimanual

Figure 2.

Intrahemispheric versus interhemispheric connectivity for the combined unimanual tasks during segment 2. Interhemispheric connectivity was greater than intrahemispheric connectivity during both performance conditions that depended on the task requirements of segment 1 (unimanual vs. bimanual).

left, unimanual right and bimanual) $\times$ condition (requirements during segment 1, which were unimanual right and bimanual for the unimanual left task; unimanual left and bimanual for the unimanual right task; unimanual left and unimanual right for the bimanual task). There was a main effect of condition [$F(1,7) = 26.9$, $P < 0.01$] and a significant task $\times$ condition interaction [$F(2,14) = 8.9$, $P < 0.01$]. Post hoc analysis revealed that coherence during the unimanual tasks was significantly lower than that from the bimanual tasks in case of unimanual requirements during segment 1 ($P < 0.05$). However, this difference disappeared when the unimanual tasks had bimanual requirements during segment 1 ($P > 0.05$), as can be noted in Figure 1. To illustrate these differences in more detail, Figure 3 shows color-coded plots of the control and switch tasks. It can be observed that functional connectivity is increased during switching as compared to control conditions, which is especially evident for the unimanual tasks when preceded by a bimanual task relative to an alternative unimanual task.

Comparing switched unimanual to bimanual control conditions. An additional analysis was performed that contrasted the switched unimanual tasks (combined) with preceding unimanual and bimanual demands to the bimanual control condition. This analysis, conducted by means of a one-way ANOVA on task, allowed to evaluate the degree of coherence change of the unimanual tasks during switching conditions. The analysis revealed a significant effect of task [$F(4,28) = 4.5$, $P < 0.01$]. Post hoc analysis showed that the unimanual tasks with previous unimanual demands did not differ from the bimanual control condition ($P > 0.05$), whereas the unimanual tasks with previ-

Figure 3.

Color-coded plots of the different motor tasks (left, right and bimanual) in the control (C) and switching (S) conditions during segment 2. For the unimanual switch tasks, this involved alternative unimanual or bimanual behaviour during segment 1, whereas it concerned unimanual left or right hand movements for the bimanual switch task. The data illustrate that the degree of functional coupling augmented during switching as compared to control conditions. Furthermore, connectivity was strongly intensified during the unimanual tasks when preceded by a bimanual rather than an alternative unimanual task during segment 1. The bimanual task was not differently affected by one or the other unimanual task during segment 1. The connectivity groupings involved intrahemispheric left (FC3-C3, FC3-CP3, FC3-P3, C3-CP3, C3-P3, CP3-P3), intrahemispheric right (FC4-C4, FC4-CP4, FC4-P4, C4-CP4, C4-P4, CP4-P4) and interhemispheric connections (FC3-FC4, C3-C4, CP3-CP4, P3-P4). Note that the distances between electrodes are not drawn to scale.

ous bimanual demands produced increased coherence as compared to the bimanual control condition ($P < 0.05$), as can be observed in Figure 1.

Segment 3

Performance conditions. For the performance conditions, the segment 3 of the serial arrangement was analysed to

examine effects due to previous history of two other tasks. All the segment 3 from the 12 task combinations were included, which resulted in four different final segments per task as a function of the preceding requirements.

Connectivity changes during switching conditions. The performance conditions of the different tasks were examined to evaluate the impact of task switching on the neural dynamics. The analyses were conducted separately for the different tasks by means of 2×2 ANOVAs on repetition (same vs. different task during segment 1) and condition (requirements during segment 2, which were unimanual right and bimanual for unimanual left task; unimanual left and bimanual for unimanual right task; unimanual left and unimanual right for bimanual task; see Fig. 4).

Unimanual left: The analysis revealed a main effect of repetition [$F(1,7) = 5.7$, $P < 0.05$]. The mean scores were 0.087 ± 0.019 and 0.104 ± 0.023 for the same and different conditions, respectively. Additional analysis demonstrated that the control task differed from the same [$t(7) = 2.6$, $P < 0.05$] and different [$t(7) = 4.5$, $P < 0.01$] conditions.

Unimanual right: The analysis showed a main effect of repetition [$F(1,7) = 8.5$, $P < 0.05$]. The mean scores were 0.092 ± 0.018 and 0.110 ± 0.020 for the same and different conditions, respectively. Additional analysis indicated that the control task differed from the same [$t(7) = 3.0$, $P < 0.05$] and different [$t(7) = 6.4$, $P < 0.01$] conditions.

Bimanual: The analysis demonstrated no significant effects ($P > 0.05$). The mean scores were 0.108 ± 0.018 and 0.103 ± 0.015 for the same and different conditions, respectively. Additional analysis suggested that these conditions combined were significantly different from the control task [$t(7) = 2.4$, $P < 0.05$].

Figure 4.

The performance conditions during segment 3 which include the task requirements of segment 1 (repetition; same vs. different task) for the different tasks: unimanual left, unimanual right and bimanual.

Comparing the different tasks during switching conditions. An additional analysis was conducted that contrasted the three different tasks. This analysis permitted to assess the impact of task repetition and task complexity upon post-switching neural dynamics, and contrasted the different motor tasks by means of a 2×3 ANOVA on repetition (same vs. different task during segment 1) and task (unimanual left, unimanual right, bimanual). The data showed a significant main effect of repetition [$F(1,7) = 11.5$, $P < 0.05$]. The repetition $\times$ task interaction was also significant [$F(2,14) = 11.1$, $P < 0.01$]. Post hoc analysis showed that both unimanual same conditions produced less coherence than the bimanual same and different conditions ($P < 0.05$), whereas both unimanual different conditions did not differ from both bimanual conditions ($P > 0.05$).

EEG Data: Power

The power analyses were performed to examine whether power modulations could have contributed to the observed coherence changes in the switching conditions.

Segment 2

The analyses were conducted separately for the different tasks by means of t -tests on condition that implicated the requirements of segment 1 (unimanual right and bimanual for the unimanual left task; unimanual left and bimanual for the unimanual right task; unimanual left and unimanual right for the bimanual task). None of the analyses reached a level of significance ($P > 0.05$). Additional correlation analyses between coherence and power changes showed no significant correlation coefficients between both variables ($P > 0.05$). The average correlations were -0.26 , 0.09 and -0.22 for unimanual left, unimanual right and bimanual, respectively.

Segment 3

The analyses were made separately for the different tasks by means of 2×2 ANOVAs on repetition (same vs. different task during segment 1) and condition (requirements during segment 2, which were unimanual right and bimanual for the unimanual left task; unimanual left and bimanual for the unimanual right task; unimanual left and unimanual right for the bimanual task). The analyses revealed no significant effects ($P > 0.05$). Additional correlation analyses between coherence and power changes demonstrated no significant correlation coefficients between both variables ($P > 0.05$). The average correlations were 0.03 , -0.02 and 0.11 for unimanual left, unimanual right and bimanual, respectively.

These results indicate that the power changes that occurred in the different switching conditions were not significantly different from one another. This implies that although modifications in power could contribute to

increases in coherence through non-linear effects [Florian et al., 1998], the observed changes in coherence due to switching were independent of power modulations.

Behavioural Data

Cycle duration was analysed to examine whether behavioural differences occurred during the various conditions. For the bimanual task, left and right hand performances were combined. Mean $\pm$ SD scores are reported.

Segment 2

The analyses were made separately for the different tasks by means of one-way ANOVAs on condition (requirements of segment 1, which were unimanual right, bimanual and control for the unimanual left task; unimanual left, bimanual and control for the unimanual right task; unimanual left, unimanual right and control for the bimanual task). None of the analyses reached a level of significance ($P > 0.05$). The mean cycle durations were 527 ± 6 ms, 523 ± 3 ms and 517 ± 10 ms for unimanual left, unimanual right and bimanual, respectively.

Segment 3

The analyses were conducted separately for the different tasks by means of 2×2 ANOVAs that involved repetition (same vs. different task during segment 1) and condition (requirements during segment 2, which were unimanual right and bimanual for the unimanual left task; unimanual left and bimanual for the unimanual right task; unimanual left and unimanual right for the bimanual task). The analyses revealed no significant effects ($P > 0.05$). The mean cycle durations were 521 ± 7 ms, 520 ± 3 ms and 518 ± 5 ms for unimanual left, unimanual right and bimanual, respectively.

DISCUSSION

Our motor repertoire enables us to perform tasks with a high degree of complexity under a variety of circumstances in a dynamic environment. Many of these activities are composed of multiple actions that are successively performed within an overall arrangement. This suggests that serial performance is characterised by the requirements of the component tasks; an issue that has received consideration since the seminal work of Lashley [1951].

In this study, the main aim was to compare the neural dynamics of motor behaviour in a multi-task compared to a single-task setting. To this end, unimanual and bimanual actions were executed according to a serial arrangement that followed a switching paradigm. Unimanual tasks were included based on the premise that movement of one limb is mainly controlled from the contralateral hemisphere. Conversely, bimanual acts, which are strongly delegated from the left hemisphere, are more complex and

require intensified information processing [Serrien et al., 2003]. Although skill complexity can be defined in a variety of ways, in the present framework it implies that the coordinative elements in the bimanual task underlie a degree of intricacy that is higher than that of unimanual tasks [Serrien et al., 2007].

Together, these arguments suggest that factors such as the performing hand and skill complexity promote distinct neural processing that will have consequences when motor tasks are performed in series. The hypothesis can be made that the serial arrangement would affect the neural dynamics due to reorganization of the existing neural activity, with task history operating as an internal constraint. In the present work, the experimental design included easy motor tasks to prevent training effects from motor learning [Krakauer et al., 2006]. The data analysis assessed switching and control (repeat) conditions by means of EEG-coherence in the β frequency band, because of its strong association with motor function [Serrien et al., 2003]. The focus of evaluation was on the motor network that underlies task performance, independent of the fact that the switch is steered from various regions such as the medial areas, prefrontal cortex, basal ganglia and parietal cortex [Deiber et al., 2001; Fuster, 2001; Jäncke et al., 2000; Kennerley et al., 2004; Tanji, 2001]. These distributed regions implicate higher-order cognitive processing for arranging the switch from the old to the new behavioural state.

Task Switching

Previously switching between tasks has been evaluated in the literature by comparing episodes which require task switching to those in which the same task is repeated [Monsell, 2003]. A common observation is that subjects react slower (and are less accurate) during switch than during repeat trials. These switch costs have been attributed to active task reconfiguration [Meiran, 1996; Rogers and Monsell, 1995] or proactive interference from past behaviour [Allport et al., 1994]. Although reduced with preparation time, switch costs are not eliminated. This indicates that they represent genuine processing demands that associate with changing tasks. It also illustrates that central rigidity exists when the response system is already engaged.

In the present study, the impact of task switching upon processing requirements was demonstrated in an alternative manner. In particular, it was revealed that the neural activity that support motor task performance was up-regulated during switch compared to control trials, even though the behavioural output was not affected. The up-regulation was observed across all performance conditions, and suggests that it reflects general demands when different movement patterns are produced in series. This adaptation may have several motives, and point to facilitatory and/or inhibitory processes. First, it is possible that preceding neural activity biases future processing. In other words, previous activity operates as a background that interferes with subsequent information processing, such

that neural activity needs to be increased for assisting movement production. For example, switching between hands implies that the hemisphere that is initially dominant for movement production becomes non-dominant. Consequently, its dynamic activation pattern makes that the hemisphere that supports motor performance after the switch needs to upgrade its neural processing in order to maintain a normal hemispheric balance in view of the latest task demands. The significance of this functional balance has especially become apparent from studies evaluating neurological disorders and aging during which activation shifts between hemispheres have been noted that can be associated with behavioural consequences [Calautti and Baron, 2003; Naccarato et al., 2006]. Second, settling of the new task requirements in combination with inhibiting the previous ones may impinge on the processing resources. In this respect, Mayr and Keele [2000] have suggested that inhibitory processes that disengage previous requirements are automatically triggered by task competition. Finally, a change in attentional focus or alertness may be sufficient to increase the processing needs. In particular, by varying attention to movement, activity in the motor network may be adapted at multiple sites [Johansson-Berg and Matthews, 2002].

The current data extend the observations from the literature that task switching not only imposes extra processing to select new task rules but also to implement and execute them. It implies that switching between tasks involves sustained effects. Furthermore, the data indicate that the neural activity associated with a particular task is influenced by the hemispheric dynamics that is present prior to its performance. This suggests that the existing hemispheric profile influences neural processing of an upcoming task. However, besides an overall increase in neural activity for switch compared to repeat tasks, the findings also revealed that task dependent factors are relevant, as discussed next. This implies that switching between motor tasks not only introduces general but also task-specific processes, supporting the existence of a control hierarchy when behavioural requirements change due to task switching.

Task Dependency and Complexity

During control conditions, the degree of functional connectivity was higher for bimanual than for unimanual tasks. This result denotes that bimanual in comparison to unimanual assignments involve extra computational demands and require increased information processing, which supports earlier work [Andres et al., 1999; Serrien et al., 2003]. However, the unimanual–bimanual difference disappeared during switching conditions. In these circumstances, the unimanual tasks required increased processing, which resulted in equivalent or additional coherence compared to a bimanual control task that required no switching. The strongest effect was observed when the unimanual tasks were preceded by a bimanual rather than alternative unimanual task. This finding proposes that

neural processing of a movement pattern within a serial arrangement is influenced by preceding task complexity. For the bimanual assignment, performing previously a unimanual task with the left or right hand did not have a differential impact. These observations indicate that unimanual compared to bimanual acts are more sensitive to pre-switching demands and suggest the importance of task history on motor performance: The more complex a particular task, the more neural effort it takes for executing a subsequent task. It implies that the contextual setting imposes constraints on the processing resources, with a stronger effect when a greater disparity exists between the previous and current task demands. In contrast to the influence of complexity, the effect of hand had less significant consequences on neural reorganization of the new assignment.

The context-dependent increase in coherence for unimanual switching conditions was largely steered by interhemispheric rather than intrahemispheric connectivity. This observation indicates that interhemispheric interactions are especially advantageous and responsive as demands on the motor system increase. It supports the idea that interhemispheric transmission assists task performance under challenging conditions (Belger and Banich, 1998). That unimanual tasks particularly call upon these pathways may be related to explicit processing that is required to prevent the opposite hemisphere from interfering with the required behaviour. In particular, specifying a unimanual skill necessitates interhemispheric communication that is directed to prevent the natural tendency toward bimanual coupling [Duque et al., 2005; Huang et al., 2004].

In conclusion, everyday tasks often require the execution of compound acts. Hence, studying the neural regulation of motor tasks performed in series provides valuable information about the control of multiple elements integrated within a global configuration. In the present work, performing a serial arrangement of unimanual and bimanual acts that required switching between tasks resulted in intensified functional connectivity, and associated with general (switching) as well as task specific (complexity) modulations. Overall, the data illustrate that the neural dynamics associated with motor behaviour assimilates past and present activity, which accordingly impacts on neural efficiency.

REFERENCES

- Allport A, Styles EA, Hsieh S (1994): Shifting intentional set: Exploring the dynamic control of tasks. In: Umiltà C, Moscovitch M, editors. *Attention and Performance*, Vol. 15: Conscious and Nonconscious Information Processing. Cambridge: MIT Press. pp 421–452.
- Andres FG, Mima T, Schulman AE, Dichgans J, Hallett M, Gerloff C (1999): Functional coupling of human cortical sensorimotor areas during bimanual skill acquisition. *Brain* 122:855–870.
- Belger A, Banich MT (1998): Costs and benefits of integrating information between the cerebral hemispheres: A computational perspective. *Neuropsychology* 12:380–398.
- Blum J, Lutz K, Jäncke L (2007): Coherence and phase locking of intracerebral activation during visuo- and audio-motor learning of continuous tracking movements. *Exp Brain Res* 182:59–69.
- Calautti C, Baron JC (2003): Functional neuroimaging studies of motor recovery after stroke in adults: A review. *Stroke* 34: 1553–1566.
- Chen JT, Lin YY, Shan DE, Wu ZA, Hallett M, Liao KK (2005): Effect of transcranial magnetic stimulation on bimanual movements. *J Neurophysiol* 93:53–63.
- Deiber MP, Caldarà R, Ibañez V, Hauert CA (2001): Alpha band power changes in unimanual and bimanual sequential movements, and during motor transitions. *Clin Neurophysiol* 112:1419–1435.
- Duque J, Mazzocchio R, Dambrosia J, Murase N, Olivier E, Cohen LG (2005): Kinematically specific interhemispheric inhibition operating in the process of generation of a voluntary movement. *Cereb Cortex* 15:588–593.
- Fecteau JH, Munoz DP (2003): Exploring the consequences of the previous trial. *Nat Rev Neurosci* 4:435–443.
- Florian G, Andrew C, Pfurtscheller G (1998): Do changes in coherence always reflect changes in functional coupling. *Electroencephalogr Clin Neurophysiol* 106:87–91.
- Foltys H, Sparing R, Boroojerdi B, Krings T, Meister IG, Mottaghy FM, Töpper R (2001): Motor control in simple bimanual movements: A transcranial magnetic stimulation and reaction time study. *Clin Neurophysiol* 112:265–274.
- Fuster JM (2001): The prefrontal cortex—An update: Time is of the essence. *Neuron* 30:313–333.
- Gerloff C, Corwell B, Chen R, Hallett M, Cohen LG (1998): The role of the human motor cortex in the control of complex and simple finger movement sequences. *Brain* 121:1695–1709.
- Huang MX, Harrington DL, Paulson KM, Weisend MP, Lee RR (2004): Temporal dynamics of ipsilateral and contralateral motor activity during voluntary finger movement. *Hum Brain Mapp* 23:26–39.
- Hummel F, Andres F, Altenmüller E, Dichgans J, Gerloff C (2002): Inhibitory control of acquired motor programmes in the human brain. *Brain* 125:404–420.
- Jäncke L, Peters M, Schlaug G, Posse S, Steinmetz H, Müller-Gärtner H (1998): Differential magnetic resonance signal change in human sensorimotor cortex to finger movements of different rate of the dominant and subdominant hand. *Brain Res Cogn Brain Res* 6:279–284.
- Jäncke L, Himmelbach M, Shah NJ, Zilles K (2000): The effect of switching between sequential and repetitive movements on cortical activation. *Neuroimage* 12:528–537.
- Johansen-Berg H, Matthews PM (2002): Attention to movement modulates activity in sensori-motor areas, including primary motor cortex. *Exp Brain Res* 142:13–24.
- Kennerley SW, Sakai K, Rushworth MF (2004): Organization of action sequences and the role of the pre-SMA. *J Neurophysiol* 91:978–993.
- Kelso JA, Scholz JP, Schöner G (1988): Dynamics governs switching among patterns of coordination in biological movement. *Phys Lett A* 134:8–12.
- Krakauer JW, Mazzoni P, Ghazizadeh A, Ravindran R, Shadmehr R (2006): Generalization of motor learning depends on the history of prior action. *PLoS Biol* 10:1798–1808.
- Lashley KS (1951): The problem of serial order in behavior. In: Jeffress LA, editor. *Cerebral Mechanisms in Behavior*. New York: Wiley.
- Mayr U, Keele SW (2000): Changing internal constraints on action: The role of backward inhibition. *J Exp Psychol Gen* 129:4–26.

- Meiran N (1996): Reconfiguration of processing mode prior to task performance. *J Exp Psychol Learn Mem Cogn* 22:1423–1442.
- Monsell S (2003): Task switching. *Trends Cogn Sci* 7:134–140.
- Naccarato M, Calautti C, Jones PS, Day DJ, Carpenter TA, Baron JC (2006): Does healthy aging affect the hemispheric activation balance during paced index-to-thumb opposition task? An fMRI study. *Neuroimage* 32:1250–1256.
- Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.
- Rogers RD, Monsell S (1995): Costs of a predictable switch between simple cognitive tasks. *J Exp Psychol General* 124:207–231.
- Serrien DJ, Brown P (2003): The integration of cortical and behavioral dynamics during initial learning of a motor task. *Eur J Neurosci* 17:1098–1104.
- Serrien DJ, Swinnen SP (1999): Intentional switching between behavioral patterns of homologous and nonhomologous effector combinations. *J Exp Psychol Hum Percept Perform* 25:1253–1267.
- Serrien DJ, Cassidy MJ, Brown P (2003): The importance of the dominant hemisphere in the organization of bimanual movements. *Hum Brain Mapp* 18:296–305.
- Serrien DJ, Pogosyan AH, Cassidy MJ, Brown P (2004): Anticipatory cortico-cortical interactions: Switching the task configuration between effectors. *Exp Brain Res* 154:359–367.
- Serrien DJ, Ivry RB, Swinnen SP (2006): Dynamics of hemispheric specialization and integration in the context of motor control. *Nat Rev Neurosci* 7:160–166.
- Serrien DJ, Ivry RB, Swinnen SP (2007): The missing link between action and cognition. *Prog Neurobiol* 82:95–107.
- Tanji J (2001): Sequential organization of multiple movements: Involvement of cortical motor areas. *Annu Rev Neurosci* 24: 631–651.
- Viviani P, Perani D, Grassi F, Bettinardi V, Fazio F (1998): Hemispheric asymmetries and bimanual asynchrony in left- and right-handers. *Exp Brain Res* 120:531–536.