Interactions between new and pre-existing dynamics in bimanual movement control

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Abstract

Motor skills are commonly acquired through practice. This process not only involves acquisition of the particular task demands but also requires overcoming pre-existing modes. In the present study, interactions between new and intrinsic dynamics were evaluated. Accordingly, bimanual finger tapping with a 2:1 ratio was performed according to two training schedules: continuous (consecutive trials) and interrupted (non-consecutive trials with intermediate 1:1 in-phase performances). In addition, in-phase and anti-phase were probed before and after training. Behavioural output was assessed by means of temporal accuracy and variability, whereas neural activation patterns were determined by EEG coherence. Results showed that continuous practice resulted in improved performance with reduced coherence across the motor network. For interrupted practice, behavioural execution ameliorated, although it was inferior to performance with continuous practice. In terms of neural changes, the degree of intrahemispheric and midline connectivity did not reduce with interrupted practice, whereas interhemispheric connectivity increased. This signifies that short-term motor consolidation of the 2:1 task was disrupted due to intermediate performance of the in-phase mode. Furthermore, the probed in-phase and anti-phase pattern showed no behavioural changes, although neural alterations occurred that depended on training schedule and coordination mode. Overall, the observations illustrate bidirectional interactions between new and inherent dynamics during motor acquisition, raising issues about effective methods for learning skills and scheduling of practices in neurorehabilitation.

Keywords: EEG, functional connectivity, coherence, motor acquisition

Introduction

Bimanual routines are part of our daily-life activities and at times involve a high degree of complexity such as playing a musical instrument. Typically, compound acts can be performed following practice during which the behaviour gains accuracy and stability. At the same time, learning-related changes occur at the neural level, reflecting greater functional efficiency and advanced movement control (Debaere et al. 2004; Doyon and Benali 2005; Haslinger et al. 2004; Puttemans et al. 2005). Overall, it is acknowledged that motor learning characterizes those internal processes that result in a relatively permanent change of skilled performance (Schmidt and Lee 2005), thus distinguishing it from adaptation or other short-lived effects. Of note is that motor learning not only necessitates the acquisition of the particular task demands but also requires overcoming the pre-existing modes (Zanone and Kelso 1992). Indeed, an inability to overrule intrinsic tendencies associates with inappropriate habits during skill acquisition (Walter et al. 1997), which may become evident through patterns of interference (Semjen 2002).

One well-known example of intrinsic behaviour is the tendency towards spatiotemporal coupling during rhythmic bimanual actions (Franz et al. 1991; Kelso et al. 1981; Swinnen et al. 1991). This preference during which both limbs move at similar tempo with synchronization at the reversal points integrates the in-phase (symmetrical) and anti-phase (asymmetrical) mode. Typical is that these configurations can be performed with high accuracy and low variability without practice (Kelso 1984). Based on the previous, it is argued that bimanual tasks are particularly valuable for evaluating the acquisition of new coordination patterns and for assessing influences of pre-existing modes. In this respect, earlier work has shown that bimanual motor training at other phases is accompanied by (temporal) destabilization of the intrinsic modes (Fontaine et al. 1997; Kelso and Zanone 2002; Rémy et al. 2008), whereas acquisition of the new task involves overcoming those intrinsic preferences (Summers 2002). This indicates that pre-existing tendencies influence the new behaviour but in return are affected by the to-be-learned task.

In general, the effect of practice has received considerable attention in motor learning studies, and researchers have employed a variety of tasks, contexts and paradigms, practice techniques as well as schedules (e.g., Bays et al. 2005; Kostrubiec et al. 2006; Krakauer et al. 2006; Shea et al. 1979; Vangheluwe et al. 2006; Wulf et al. 1994). This line of research has pointed to two factors that in particular seem to impact on the training conditions: (1) the number of tasks or task variations practiced and (2) the order in which the tasks are trained. The present study builds upon this knowledge by evaluating the training of a well-defined motor task according to two practice schedules that integrate pre-existing behaviour. In particular, acquisition of a bimanual finger tapping task with a 2:1 frequency ratio is examined. This assessment is based on behavioural findings that have shown that this assignment involves intermittent periods of attraction towards pre-existing modes (Summers 2002). Furthermore, the 2:1 task permits a strategy that involves both effectors to alternate between simultaneous and separate responses. Although this manner of implementation represents a simplified tactic to comply with the coordinative demands, it introduces an alternating process of facilitation during which both effectors move together (in-phase) and inhibition during which one effector moves while the other is prevented from moving. In this work, two types of evaluations are being made in order to determine competition between new and pre-existing dynamics. First, it is examined how practice of a new task (multifrequency = 2:1 coordination) affects its neural activity and that of the intrinsic modes (isofrequency = in-phase and anti-phase coordination). Second, it is assessed to what extent the training schedule (continuous = consecutive 2:1 practice vs. interrupted = non-consecutive 2:1 practice with intermediate in-phase performances) evokes distinct changes in the task's neural regulation. As the in-phase mode partly operates as an attractor and partly as a distractor for the multifrequency task requirements, the suggestion is made that intermediate in-phase executions will cause interference with the 2:1 training schedule. To assess the neural dynamics of motor acquisition and its adaptability, the data analysis focuses on EEG coherence, which expresses functional communication between brain areas.

Methods

Participants and tasks

Two groups of eight right-handed individuals (group1: age: 26 ± 4 years, group 2:

age: 25 ± 3 years, 2 males and 6 females in each group) as determined by the Edinburgh handedness inventory (Oldfield 1971) participated in the experiment. Inventory scores from both groups were not significantly different from one another ($P > .05$). In accordance with the declaration of Helsinki, the participants gave informed consent to take part in the study, which was approved by the local ethics committee. The participants were randomly assigned to a group and were asked to perform bimanual tapping using their index fingers on a keyboard according to a 2:1 mode (new behaviour), in-phase or anti-phase mode (pre-existing behaviour). For the 2:1 task, which required tapping with one finger at twice the rate of the other finger, subjects were asked to use a performance strategy that involved moving both fingers simultaneously for one tap, followed by a subsequent tap of the fast finger while holding the slow finger stationary at peak upward position. In terms of timing arrangement, the non-dominant (left) finger adopted the faster tempo as the dominant (right) finger took on the slower tempo. According to this scheme, the timing demands of the non-dominant effector prevail, making the bimanual performance more difficult than the reverse arrangement (Semjen 2002). Although both effectors have distinct timing goals, it is assumed that the timekeeper is established at the frequency of the faster moving one (Semjen 2002). Timing was externally paced, and the metronome beat was set at 545 msec, which guided the fast tempo during the 2:1 trials and the tempo during the in-phase as well as anti-phase trials. There were about 60 taps per trial (metronome guided).

The training schedules which consisted of a pre, practice and post session are depicted in Figure 1. Both groups received distinct practice of the 2:1 task. Group 1 performed 2:1 trials (n=10) that were interspersed with in-phase trials (n=4) in order to interrupt motor practice, whereas group 2 executed 2:1 trials (n=14) repeatedly in order to optimize motor practice. Both groups completed similar pre and post sessions. In particular, the pre session consisted of in-phase and anti-phase trials (counterbalanced order across subjects) for probing their intrinsic nature. The post session comprised retention trials that followed training of the 2:1 task after a 10 min break. This session included 2:1, in-phase and anti-phase trials. During retention, the 2:1 task was always performed first followed by the in-phase and anti-phase trials (counterbalanced order across subjects). There were small breaks in between trials for avoiding fatigue and loss of attention. Participants were told in advance of the upcoming task requirements. They were advised to tap as smoothly as possible. A rest condition was also recorded that comprised listening to the tones of the metronome.

Insert Figure 1 about here

EEG recordings and data analysis

Continuous EEG was recorded using the Electrical Geodesics Inc. 128-channel system, and data processing was carried out using BESA software (MEGIS Software GmbH, Gräfelfing, Germany). EEG signals were amplified, band-pass filtered 0.05 Hz–100 Hz, and sampled at 250 Hz with a vertex reference. Epochs contaminated by artifacts such as eye movements and EMG-related activity were corrected for or rejected after baseline correction.

EEG coherence was used to assess functional connectivity between brain areas in the frequency domain, and was estimated by means of complex demodulation set to a frequency resolution of 2 Hz and temporal resolution of 25 msec. Background coherence acquired during rest was subtracted from coherence obtained during motor conditions. This method, which gives an estimate of task-related coherence, reduces the effects of volume conduction, between-subject differences as well as between-electrode variability, and minimizes the bias introduced by the reference electrode. As a normalized measurement of coupling between two signals at any given frequency, coherence varies between 0 (no correlation) and 1 (perfect correlation).

To measure indices of cortical activity, a region of interest approach was adopted that focused on a restricted number of electrodes. The electrodes were selected based on earlier EEG studies of movement control (Hummel et al. 2002; Serrien 2009) and were estimated to overlie premotor, sensorimotor, superior parietal and mesial areas, including supplementary motor area (SMA). The division of electrodes resulted in 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), interhemispheric (FC3-FC4, C3-C4, CP3-CP4, P3-P4) and midline (FCz-CPz). Coherence was evaluated in the beta frequency band (>12-30 Hz) due to its importance for motor behaviour (Gerloff et al. 1998; Serrien et al. 2003). Before statistical operations were conducted, coherences were transformed using the inverse hyperbolic tangent to stabilize variances. Separate analyses were conducted for the different connectivity groupings. In addition, EEG task-related power (obtained by subtracting rest from the corresponding motor conditions) was measured in the beta band at the individual electrodes, and stabilized by logarithmic transformation. Subsequently, power was analyzed in conjunction with coherence measurements in order to evaluate whether changes in power could have contributed to the modulations in coherence. Non-significant effects would indicate that the motor system effectively responded by adjusting information flow between cortical regions. Mean ± SD scores are presented in the Results section.

As illustrated in Figure 1, both groups performed 3 consecutive sessions; pre, practice and post. The main analyses were conducted for both groups separately and included the pre session (in-phase, anti-phase), practice session (start trial 1, end trial 14) and post session (2:1, in-phase, anti-phase). Furthermore, analyses were carried out that contrasted both groups on practice trial 10 of the 2:1 task, which involved trial 14 for group 1 (interrupted practice) and trial 10 for group 2 (continuous practice). Also, the start practice trial of both groups was compared.

Behavioural recordings and analysis

E-Prime software (Psychology Software Tools Inc., Pittsburgh, USA) was used to record the cycle durations in the various conditions. The metronome pace of 545 msec provided a reference signal for all motor tasks. The analysis included temporal accuracy with respect to the 2:1 and 1:1 ratio between both hands. Moreover, the deviation from the ideal value (1 or 2) was estimated for the corresponding finger taps, and accordingly averaged per trial in order to capture goal achievement of the coordinative demands. As a measurement of temporal variability, the coefficient of variation (CV) of both hands was computed as the standard deviation in timing divided by the mean tempo.

Statistical analysis

The data were analyzed using the Statistica software (StatSoft Inc., Tulsa, USA). Adjustments were made in case of violation of the sphericity assumption by using the Greenhouse-Geisser procedure. Post hoc testing included corrections with respect to multiple comparisons.

Results

Group 1: Interrupted practice of the 2:1 task

This group carried out the 2:1 task (n=10 trials) while in-phase movements (n=4 trials) were intermediately performed to disturb motor practice (Figure 1).

1. Practice of the 2:1 task

Behavioural timing. Accuracy and variability scores were calculated (Figure 2A). *Accuracy*: A one-way ANOVA on session (start practice, end practice, post) revealed a significant effect, $F(2,14) = 4.34$, $P < .05$. Post-hoc analysis showed that timing accuracy at the start of practice was lower than that obtained at the end of practice and at the post session ($P < .05$ for both). *Variability*: A two-way ANOVA on session (start practice, end practice, post) and effector (left, right) demonstrated a significant main effect of session, $F(2,14) = 18.32$, $P < .01$. Post-hoc analysis showed that timing variability at the start of practice was higher than at the end of practice and at the post session ($P < .01$ for both). There was also a main effect of effector, $F(1,7) = 21.52$, $P < .01$, with higher variability scores for the left (.055 ± .013) than right finger (.050 ± .011).

EEG coherence. One-way ANOVA's on session (start practice, end practice, post) for the different connectivity groupings revealed distinct observations (Figure 2B). In particular, no significant effect was observed for intrahemispheric left or right, or midline connectivity, $P > .05$. In contrast, the ANOVA for interhemispheric connectivity was significant, $F(2,14) = 5.41$, $P < .05$. Post-hoc analysis indicated increased coherence during the end and post sessions as compared to the start session ($P < .05$ for both).

EEG power. Correlation analyses between the coherence scores of the interhemispheric couplings and the power scores of the individual electrodes showed no significant effects, $P > .05$. The mean correlation coefficients for start, end and post trials were .05, .16 and .18, respectively.

Insert Figure 2 about here

2. Probing of the in-phase task during pre and post sessions

Behavioural timing. Accuracy and variability scores were estimated. *Accuracy:* The paired *t*-test on session (pre, post) revealed no significant effect, $P > .05$. The mean scores were .007 ± .001 and .010 ± .003 for pre and post trials, respectively. *Variability:* A two-way ANOVA on session (pre, post) and effector (left, right) showed no significant effects, $P > .05$. The mean scores were .036 ± .007 and .038 ± .008 for pre and post trials, respectively.

EEG coherence. The *t*-tests on session (pre, post) for the different connectivity groupings indicated no significant effects, $P > .05$ (Figure 3A).

3. Probing of the anti-phase task during pre and post sessions

Behavioural timing. Accuracy and variability scores were calculated. *Accuracy*: The paired *t*-test on session (pre, post) demonstrated no significant effect, $P > .05$. The mean scores were .012 ± .002 and .014 ± .004 for pre and post trials, respectively. *Variability:* A two-way ANOVA on session (pre, post) and effector (left, right) revealed no significant effects, $P > .05$. The mean scores were .040 ± .09 and .041 ± .012 for pre and post trials, respectively.

EEG coherence. The *t*-tests on session (pre, post) for the various connectivity groupings showed divergent results (Figure 3B). In particular, no significant effect was observed for intrahemispheric left or right connectivity, $P > .05$. In contrast, significance was noted for interhemispheric [$t(7) = 3.36$, $P < .05$], and for midline connectivity [$t(7) = 2.42$, $P < .05$], suggesting increased coherence in the post than pre session.

EEG power. Correlation analyses between the coherence scores of the interhemispheric-midline couplings and the power scores of the individual electrodes showed no significant effects, *P* > .05. The mean pre-post scores were .08, .21 for interhemispheric, .02 and -.12 for midline connectivity.

Insert Figure 3 about here

Group 2: Continuous practice of the 2:1 task

This group received continuous practice of the 2:1 pattern (n=14 trials) to optimize motor practice (Figure 1).

1. Practice of the 2:1 task

Behavioural timing. Accuracy and variability scores were determined (Figure 4A). *Accuracy:* A one-way ANOVA on session (start practice, end practice, post) illustrated a significant effect, *F*(2,14) = 7.56, *P* < .01. Post-hoc analysis showed that timing accuracy improved from start to end and post sessions (*P* < .05 for both). *Variability*: A two-way ANOVA on session (start practice, end practice, post) and effector (left, right) indicated a significant main effect of session, *F*(2,14) = 37.74, *P* < .01. Post-hoc analysis revealed that timing variability at the start of practice was higher than at the end of practice and at the post session (*P* < .01 for both). There was also a main effect of effector, *F*(1,7) = 18.54, *P* < .01, with higher variability scores for the left (.052 ± .010) than right finger (.048 ± .012).

EEG coherence. One-way ANOVA's on session (start practice, end practice, post) for the different connectivity groupings pointed to similar observations with reduced coherence due to practice (Figure 4B). In particular, significance effects were noted for intrahemispheric left [*F*(2,14) = 5.15, *P* < .05], intrahemispheric right [*F*(2,14) = 4.46, *P* < .05], interhemispheric [*F*(2,14) = 5.51, *P* < .05], and for midline connectivity [*F*(2,14) = 5.49, *P* < .05]. Post-hoc analyses indicated higher coherence scores during start than end and post sessions (*P* < .05 for all).

EEG power. Correlation analyses between the coherence scores of the intrahemispheric left-right, interhemispheric and midline couplings to the power scores of the individual electrodes showed no significant effects, *P* > .05. The mean scores for start, end and post trials were -.24, .06 and .03 for intrahemispheric left, -.10, -.23 and -.14 for intrahemispheric right, -.22, .17 and .13 for interhemispheric, -.20, .11 and .15 for midline connectivity.

Insert Figure 4 about here

2. Probing of the in-phase task during pre and post sessions

Behavioural timing. Accuracy and variability scores were estimated. *Accuracy*: The *t*-test on session (pre, post) exposed no significant effect, *P* > .05. The mean scores were .009 ± .002 and .011 ± .003 for pre and post trials, respectively. *Variability:* A two-way ANOVA on session (pre, post) and effector (left, right) showed no significant effects, *P* > .05. The mean scores were .034 ± .009 and .037 ± .007 for pre and post trials, respectively.

EEG coherence. The *t*-tests on session (pre, post) for the various connectivity groupings indicated distinctive results (Figure 5A). In particular, no significant effect was observed for intrahemispheric left or right, or midline connectivity, *P* > .05. Conversely, significance of the *t*-test was noted for interhemispheric connectivity with higher coherence in the post than pre session, *t*(7) = 2.47, *P* < .05.

EEG power. Correlation analyses between the coherence scores of the interhemispheric couplings and the power scores of the individual electrodes showed no significant effects, *P* > .05. The mean pre-post scores were .07 and .12.

3. Probing of the anti-phase task during pre and post sessions

Behavioural timing. Accuracy and variability scores were calculated. *Accuracy*: The *t*-test on session (pre, post) showed no significant effect, *P* > .05. The mean scores were .014 ± .003 and .013 ± .004 for pre and post trials, respectively. *Variability:* A two-way ANOVA on session (pre, post) and effector (left, right) showed no significant effects, *P* > .05. The mean scores were .039 ± .011 and .040 ± .010 for pre and post trials, respectively.

EEG coherence. The *t*-tests on session (pre, post) for the different connectivity groupings showed differential outcomes (Figure 5B). In particular, no significant effect was noted for intrahemispheric left or right connectivity, *P* > .05. Conversely, there was a significant effect for interhemispheric [*t*(7) = 2.46, *P* < .05], and for midline connectivity [*t*(7) = 3.15, *P* < .05], pointing to increased coherence in the post than pre session.

EEG power. Correlation analyses between the coherence scores of the interhemispheric-midline couplings and the power scores of the individual electrodes showed no significant effects, *P* > .05. The mean pre-post scores were .10, -.09 for interhemispheric, .19 and -.11 for midline connectivity.

Insert Figure 5 about here

<u>Group comparison of the 2:1 task</u>

Analyses were conducted on practice trial 10 of the 2:1 task, which involved trial 14 for group 1 (interrupted practice) and trial 10 for group 2 (continuous practice). In addition, a group comparison was made for the start practice trial.

Behavioural timing. Accuracy and variability scores were determined. *Accuracy:* The independent *t*-test (group 1, group 2) on practice trial 10 revealed a significant effect [*t*(14) = 2.70, *P* < .05], with group 1 being less accurate than group 2. The mean scores were .017 ± .005 and .013 ± .003 for group 1 and 2, respectively. The start practice trial from both groups was not significantly different from one another, *P* > .05. Expressed as percentage scores, the data suggested that practice improved temporal accuracy with 19% for group 1 and with 35% for group 2. *Variability*: A two-way ANOVA on group (group 1, group 2) and effector (left, right) indicated a significant main effect of group, *F*(1,14) = 21.40, *P* < .01. The mean scores were .053 ± .015 and .047 ± .013 for group 1 and 2, respectively. In percentage scores, the observations implied that practice improved temporal variability with 11% for group 1 and with 23% for group 2. The main effect of effector was also significant, *F*(1,7) = 5.76, *P* < .05, with higher variability scores for the left (.051 ± .014) than right finger (.049 ± .010).

EEG coherence. The independent *t*-tests (group 1, group 2) for the different connectivity couplings on practice trial 10 demonstrated significant effects for all analyses, with group 1 having higher coherences than group 2 (Figure 6). In particular, significant effects were noted for intrahemispheric left [$t(14) = 2.22$, $P < .05$], intrahemispheric right [$t(14) = 2.34$, $P < .05$], interhemispheric [$t(14) = 2.95$, $P < .01$], and for midline connectivity [$t(14) = 2.17$, $P < .05$]. The start practice trial of both groups (illustrated in Figures 2B and 4B) showed no significant effects for intrahemispheric left [$t(14) = 0.61$, $P > .05$], intrahemispheric right [$t(14) = 0.09$, $P > .05$], interhemispheric [$t(14) = 0.72$, $P > .05$], or midline connectivity [$t(14) = 0.23$, $P > .05$].

Insert Figure 6 about here

Discussion

An important constraint during interlimb coordination is the tendency toward spatiotemporal coupling, which is observed during discrete as well as rhythmic movements (e.g., Kelso et al. 1979, 1981). With respect to rhythmical patterns, this preference manifests itself through a 1:1 frequency ratio that is performed according to an in-phase (symmetrical) or anti-phase (asymmetrical) mode. It consequently reflects pre-existing behaviour that can be efficiently executed without any training. Conversely, complex actions that involve polyrhythms or unfamiliar phase relations require practice and are susceptible to interference from the preferred modes (Serrien and Swinnen 1997; Zanone and Kelso 1992). With training, competitive influences from the intrinsic modes disappear during which the new task gains in accuracy and stability. In the present study, training of a motor task with a 2:1 frequency ratio was examined under continuous vs. interrupted practice condition. It was argued that the arrangement of the practice scheme would affect the learning potential due to interactions between new and pre-existing dynamics. Here, motor practice was assessed during the fast learning stage during which significant performance improvements are noticeable within a training session.

The 2:1 task: New motor acquisition and the effect of continuous vs. interrupted practice

Bimanual tapping according to a 2:1 ratio implies a simple metrical organization with an explicit representation of temporal goals (Semjen 2002). Due to the particular task demands, the 2:1 arrangement supports a strategy that allows the effectors to move simultaneously for one tap where after the fast effector continues to tap once while the slow effector pauses at peak extension. Therefore, in-phase movements act as an attractor as well as a distractor for the 2:1 task requirements. Accordingly, the hypothesis was made that in-phase trials introduced during a 2:1 training schedule would disturb the normal acquisition process.

The results from the continuous practice group revealed improved behavioural performance along with reduced functional connectivity across the designated network, which underlines that the short training period associated with an enhanced motor experience. This observation denotes that practice-driven plasticity results in efficient inter-regional communication. With interrupted practice, the subjects' behavioural output improved, although it was inferior compared to that from continuous practice with the 2:1 task, indicating that the in-phase mode interfered with the refinement of the new assignment. In terms of neural activity, there was unchanged intrahemispheric and midline connectivity in addition to increased interhemispheric connectivity. This mixed pattern implies that the interrupted training scheme modified the functional couplings in specific ways. Especially, the augmented coherence is of particular interest and underscores the necessity of additional information processing, including attentional focusing (Johansson-Berg and Matthews 2002; Rowe et al. 2002), for supporting bimanual behaviour under challenging conditions. It should be mentioned, however, that the training schedule of the interrupted practice group also implicated the succession of two tasks in close temporal proximity. Accordingly, an inability to switch efficiently between motor acts might have contributed to the observations.

The findings from the interrupted practice group illustrate an impact of one task performance on another, with the in-phase mode having a degrading influence on the practiced 2:1 mode; an effect that was present at the end of training and at retention. The latter observation appears at variance with behavioural data that have shown that random practice (during which trials of tasks are interleaved) provide superior performance at retention as compared to blocked practice (during which trials of tasks are executed separately) (Lee and Magill 1985; Shea and Morgan 1979). This effect of contextual interference implies that practice conditions that involve a relatively high degree of interference due to a variety of motor experiences will benefit learning as observed in retention or transfer conditions (Maslovat et al. 2004). Conversely, the current findings support specificity of learning during which skills are trained according to sensorimotor context (Proteau et al. 1992). In the present paradigm, the effect of practice specificity is likely due to the particular combination of new alongside pre-existing tasks, and was additionally confirmed from the reduced performance of the interrupted vs. continuous practice group on an equal number of training trials. This finding underlines that pre-existing dynamics interferes, at least initially, with the progress of new compound actions.

Probing the in-phase and anti-phase pattern before and after 2:1 training

Isofrequency coordination according to an in-phase or anti-phase mode refers to intrinsic behaviour. Due to its more complex (asymmetrical) task demands, the anti-phase pattern is usually less successfully performed than the in-phase pattern. Overall, the relative simplicity of the in-phase mode guarantees stable motor performance under normal and perturbed conditions (Fink et al. 1999; Sadato et al. 1997; Serrien and Brown 2002). In the present study, the pre-existing modes were evaluated in order to find out whether new training modified their output and regulation. The results showed that behavioural performance was not affected. However, neural activation patterns were distinctly influenced, depending on training schedule and coordination mode. Of interest was that specific connectivity profiles showed increased activation, which likely reflected compensatory processes at the network level to maintain behavioural output.

For continuous practice, during which in-phase and anti-phase movements were performed before and after 2:1 training, interhemispheric connectivity (for in-phase and anti-phase) and midline connectivity (for anti-phase) increased from pre to post trials, pointing to augmented information processing due to new acquisition. This observation highlights a stronger perturbing effect on the anti-phase than in-phase mode, which underlines the robustness of the latter as compared to former configuration. For interrupted practice, the in-phase mode, which was intermediately performed during 2:1 training, maintained its degree of functional couplings. Conversely, the anti-phase mode, performed only at pre and post trials, showed increased interhemispheric and midline coherence due to new practice. Together, these findings extend fMRI data (Rémy et al. 2008) by detailing the functional connectivity pathways of the motor network that are responsive to new acquisition.

The combined results from the practiced 2:1 and intrinsic 1:1 modes indicate that both influence one another, depending on practice scheme and task characteristics. According to Zanone and Kelso (1992), competition between new and pre-existing behaviour shapes skill acquisition, suggesting bidirectional influences between both dynamics. This principle of competition is partly similar to the concepts of retrograde interference (influence of new on previous learning) and anterograde interference (influence of previous on new learning) when consolidating newly acquired skills (Brashers-Krug et al. 1996; Krakauer et al. 2005). Noteworthy is that the influence from pre-existing to new dynamics appeared more powerful than vice versa. This became evident from the combined practice conditions that showed behavioural in addition to neural changes for the 2:1 assignment, whereas only neural adaptations emerged for the 1:1 tasks.

Significance of interhemispheric and midline connectivity during bimanual coordination

Relevant in the present study was to identify the functional couplings that are most responsive to practice of bimanual skill. The data indicated that interhemispheric and midline couplings were most affected while intrahemispheric couplings were less involved. This finding underlines that bilaterally delegated interactions are particularly important in coordinating the processing demands when exigencies on the motor system increase. First, with respect to interhemispheric connectivity, it is acknowledged that it undertakes a decisive influence in bimanual behaviour (Grefkes et al. 2008), which may associate with computational complexity or information transfer/suppression between both hemispheres (Belger and Banich 1998; Duque et al. 2005; Kinsbourne 1970; Nowicka et al. 1996). Second, it is recognized that medial areas (including SMA) are crucial for coordinated behaviour (Grefkes et al. 2008), which may relate to demands of complexity, inhibition and timing, or subjective task experience (e.g., Chen et al. 1995; Erdler et al. 2001; Macar and Vidal 2002; Sadato et al. 1997; Serrien et al. 2002). Of note is that the significance of interhemispheric and midline areas in challenging conditions may also be due to their ability to modulate each others' activity (Grefkes et al. 2008; Serrien et al. 2002; Stancák et al. 2003).

Conclusion. Motor skills are generally learned through practice. This progression not only involves acquisition of the particular task demands but also requires overcoming pre-existing modes. By evaluating different training schedules, the present study showed bidirectional influences between both task dynamics, with a stronger impact from pre-existing to new behaviour than vice versa. These results propose that the particular arrangement of new and intrinsic tasks during training affects optimization of motor learning, which may have significant implications for scheduling practice and behavioural interventions during neurorehabilitation.

References

Bays PM, Flanagan JR, Wolpert DM (2005) Interference between velocity-dependent and position-dependent force-fields indicates that tasks depending on different kinematic parameters compete for motor working memory. Exp Brain Res 63:400-405

Belger A, Banich MT (1998) Costs and benefits of integrating information between the cerebral hemispheres: a computational perspective. Neuropsychology 12:380-398

Brashers-Krug T, Shadmehr R, Bizzi E (1996) Consolidation in human motor memory. Nature 382:252-255

Chen YC, Thaler D, Nixon PD, Stern CE, Passingham RE (1995) The functions of the medial premotor cortex. II. The timing and selection of learned movements. Exp Brain Res 102:461-473

Debaere F, Wenderoth N, Sunaert S, Van Hecke P, Swinnen SP (2004) Changes in brain activation during the acquisition of a new bimanual coordination task. Neuropsychologia 42:855-867

Doyon J, Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor skills. Curr Opin Neurobiol 15:161-167

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

Erdler M, Windischberger C, Lanzenberger R, Edward V, Gartus A, Deecke L, Beisteiner R (2001) Dissociation of supplementary motor area and primary motor cortex in human subjects when comparing index and little finger movements with functional magnetic resonance imaging. Neurosci Lett 313:5-8

Fink GR, Marshall JC, Halligan PW, Frith CD, Driver J, Frackowiak RSJ, Dolan RJ (1999) The neural consequences of conflict between intention and the senses. Brain 122:497-512

Fontaine RJ, Lee TD, Swinnen SP (1997) Learning a new bimanual coordination pattern: reciprocal influences of intrinsic and to-be-learned patterns. Can J Exp Psychol 51:1-9

Franz EA, Zelaznik HN, McCabe G (1991) Spatial topological constraints in a bimanual task. Acta Psychol 77:137-151

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

Grefkes C, Eickhoff SB, Nowak DA, Dafotakis M, Fink GR (2008) Dynamic intra- and interhemispheric interactions during unilateral and bilateral hand movements assessed with fMRI and DCM. Neuroimage 41:1382-1394

Haslinger B, Erhard P, Altenmüller E, Hennenlotter A, Schwaiger M, Gräfin von Einsiedel H, Rummeny E, Conrad B, Ceballos-Baumann AO (2004) Reduced recruitment of motor association areas during bimanual coordination in concert pianists. Hum Brain Mapp 22: 206-215

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

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

Kelso JA (1984) Phase transitions and critical behavior in human bimanual coordination. Am J Physiol Regul Integr Comp Physiol 246:R1000-R1004

Kelso JA, Holt KG, Rubin P, Kugler PN (1981) Patterns of human interlimb coordination emerge from the properties of non-linear, limit cycle oscillatory processes: theory and data. J Mot Behav 13:226-261

Kelso JAS, Southard DL, Goodman D (1979) On the coordination of two-handed movements. J Exp Psychol Hum Percept Perform 5:229-238

Kelso JA, Zanone PG (2002) Coordination dynamics of learning and transfer across different effector systems. J Exp Psychol Hum Percept Perform 28:776-797

Kinsbourne M (1970) The cerebral basis of lateral asymmetries in attention. Acta Psychol 33:193-201

Kostrubiec V, Tallet J, Zanone PG (2006) How a new behavioral pattern is stabilized with learning determines its persistence and flexibility in memory. Exp Brain Res 170:238-244

Krakauer JW, Ghez C, Ghilardi MF (2005) Adaptation to visuomotor transformations: consolidation, interference, and forgetting. J Neurosci 25:473-478

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

Lee TD, Magill RA (1985) Can forgetting facilitate skill acquisition? In Goodman D, Wilberg RB, Franks IM (eds) Differing perspectives in motor learning, memory, and control. Elsevier, Amsterdam, pp 3–22.

Macar F, Vidal F (2002) Time processing reflected by EEG surface Laplacians. Exp Brain Res 145:403-406.

Maslovat D, Chus R, Lee TD, Franks IM (2004) Contextual interference: single task versus multi-task learning. Motor Control 8:213-233

Nowicka A, Grabowska A, Fersten E (1996) Interhemispheric transmission of information and functional asymmetry of the human brain. Neuropsychologia 34:147-151

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97-113

Proteau L, Marteniuk RG, Lévesque LA (1992) Sensorimotor basis for motor learning: evidence indicating specificity of practice. Q J Exp Psychol A 44: 557-575

Puttemans V, Wenderoth N, Swinnen SP (2005) Changes in brain activation during the acquisition of a multifrequency bimanual coordination task: from the cognitive stage to advanced levels of automaticity. J Neurosci 25:4270-4278

Rémy F, Wenderoth N, Lipkens K, Swinnen SP (2008) Acquisition of a new bimanual coordination pattern modulates the cerebral activations elicited by an intrinsic pattern: an fMRI study. Cortex 44:482-493

Rowe J, Friston K, Frackowiak R, Passingham R (2002) Attention to action: specific modulation of corticocortical interactions in humans. Neuroimage 17:988-998

Sadato N, Yonekura Y, Waki A, Yamada H, Ishii Y (1997) Role of the supplementary motor area and the right premotor cortex in the coordination of bimanual finger movements. J Neurosci 17:9667-9674

Schmidt RA, Lee TD (2005) Motor control and learning: A behavioral emphasis. Human Kinetics, Champaign.

Semjen A (2002) On the timing basis of bimanual coordination in discrete and continuous tasks. Brain Cogn 48:133-148

Serrien DJ (2009) Functional connectivity patterns during motor behaviour: The impact of past on present activity. Hum Brain Mapp 30:523-531

Serrien DJ, Brown P (2002) The functional role of interhemispheric synchronization in the control of bimanual timing tasks. Exp Brain Res 147:268-272

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, Strens LHA, Oliviero A, Brown P (2002) Repetitive transcranial magnetic stimulation over the supplementary motor area (SMA) degrades bimanual movement control in humans. Neurosci Lett 328:89-92

Serrien DJ, Swinnen SP (1997) Coordination constraints induced by effector combination under isofrequency and multifrequency conditions. J Exp Psychol Hum Percept Perform 23:493-1510

Shea JB, Morgan RL (1979) Contextual interference effects on the acquisition, retention, and transfer of a motor skill. J Exp Psychol Learn Mem Cogn 5:179-187

Summers JJ (2002) Practice and training in bimanual coordination tasks: strategies and constraints. Brain Cogn 48:66-178

Stancák A, Svoboda J, Rachmanová R, Vrána J, Králík J, Tintera J (2003) Desynchronization of cortical rhythms following cutaneous stimulation: effects of stimulus repetition and intensity, and of the size of corpus callosum. Clin Neurophysiol 114:1936-1947

Swinnen SP, Young DE, Walter CB, Serrien DJ (1991) Control of asymmetrical bimanual movements. Exp Brain Res 185:163-173

Vangheluwe S, Suy E, Wenderoth N, Swinnen SP (2006) Learning and transfer of bimanual multifrequency patterns: effector-independent and effector-specific levels of movement representation. Exp Brain Res 170: 543-554

Walter CB, Swinnen SP, Corcos DM, Pollatou E, Pan HY (1997) Coping with systematic bias during bilateral movement. Psychol Res 60:202-213

Wulf G, Lee TD, Schmidt RA (1994) Reduced knowledge of results about relative versus absolute timing: Differential effects on learning. J Mot Behav 26:362-369

Zanone PG, Kelso JA (1992) Evolution of behavioral attractors with learning: nonequilibrium phase transitions. J Exp Psychol Hum Percept Perform 18:403-421

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Figure Caption

Figure 1. The training schedule of group 1 (interrupted practice of 2:1 task) and group 2 (continuous practice of 2:1 task) consisted of pre, practice and post sessions. Whereas group 1 performed 2:1 trials interspersed with in-phase trials, group 2 executed 2:1 trials repeatedly. Both groups completed similar pre and post sessions. The pre session consisted of in-phase and anti-phase trials. The post session comprised retention trials that followed practice of the 2:1 task after a 10 min break. This session included 2:1, in-phase and anti-phase trials. The 2:1 configuration was always performed first followed by the in-phase and anti-phase trials. The order of the in-phase and anti-phase modes in the pre and post sessions was counterbalanced across subjects.

Figure 2. The 2:1 task with interrupted practice. (A) behavioural accuracy (left panel: Deviation of 2:1 ratio) and variability (right panel: Coefficient of variation) and (B) coherence for the different functional couplings (intrahemispheric left, intrahemispheric right, interhemispheric and midline). Start, end and post trials are depicted. Error bars denote SDs from the means, (*) indicate significance between start vs. end practice and post sessions.

Figure 3. Coherence scores associated with the in-phase (A) and anti-phase (B) mode for the different functional couplings (intrahemispheric left, intrahemispheric right, interhemispheric and midline) during pre and post trials when performing interrupted 2:1 practice. Error bars denote SDs from the means, (*) indicate significance between pre and post sessions.

Figure 4. The 2:1 task with continuous practice. (A) behavioural accuracy (left panel: Deviation of 2:1 ratio) and variability (right panel: Coefficient of variation), and (B) coherence for the different functional couplings (intrahemispheric left, intrahemispheric right, interhemispheric and midline). Start, end and post trials are shown. Error bars denote SDs from the means, (*) indicate significance between start vs. end practice and post sessions.

Figure 5. Coherence scores associated with the in-phase (A) and anti-phase (B) mode for the different functional couplings (intrahemispheric left, intrahemispheric right, interhemispheric and midline) during pre and post trials when performing continuous 2:1 practice. Error bars denote SDs from the means, (*) indicate significance between pre and post sessions.

Figure 6. Coherence scores linked with practice trial 10 for the different functional couplings (intrahemispheric left, intrahemispheric right, interhemispheric and midline) performed by group 1 (interrupted 2:1 practice) and 2 (continuous 2:1 practice). Error bars denote SDs from the means, (*) indicate significance between groups.

Fig. 1

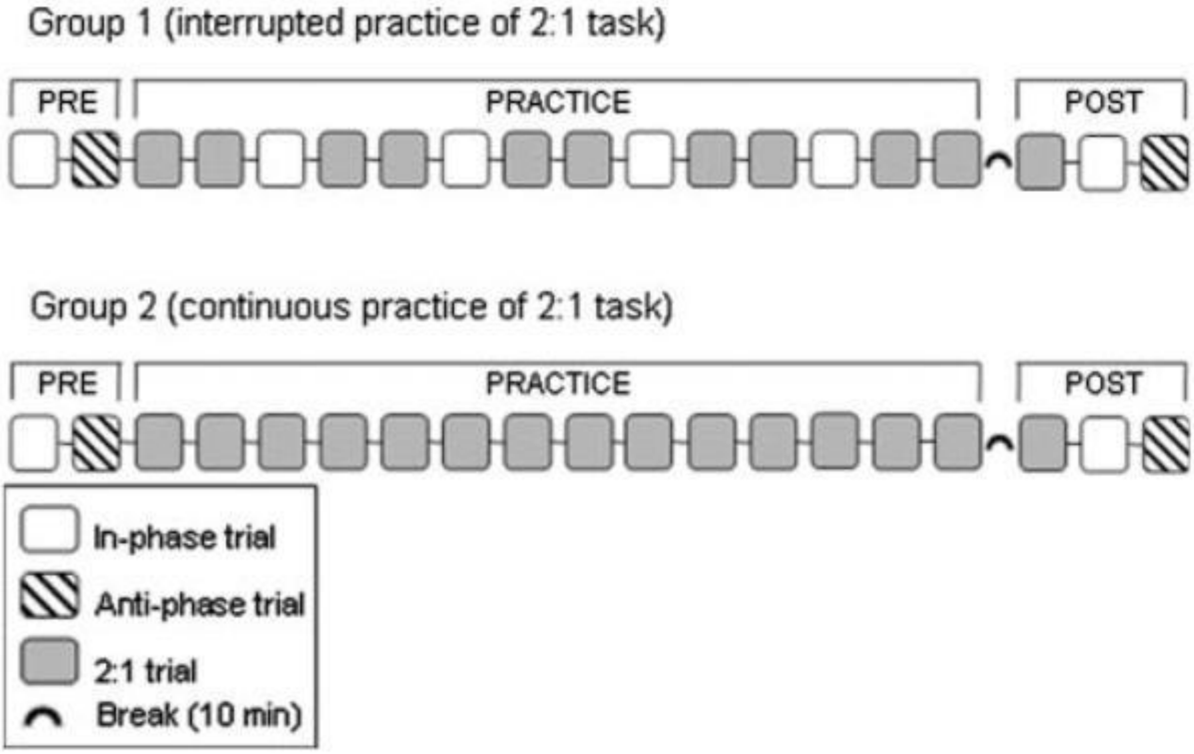
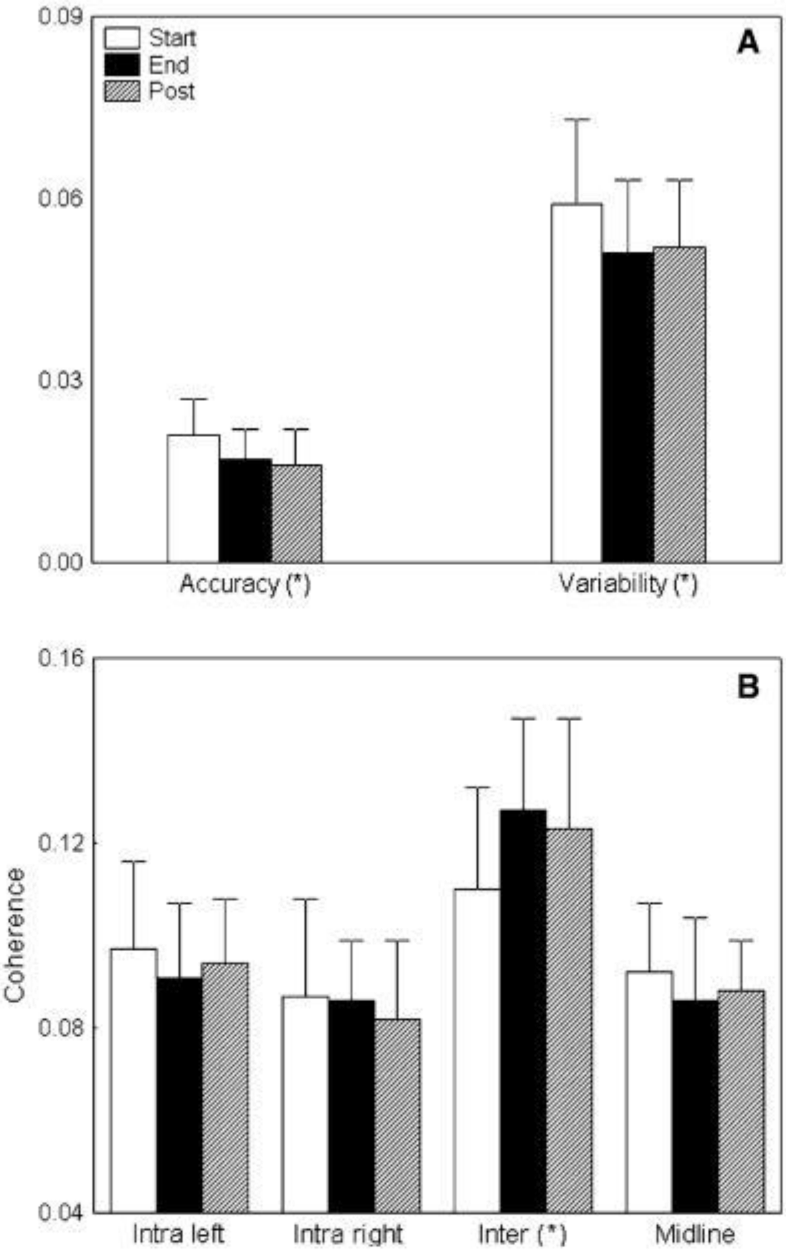

Group 1 (interrupted practice of 2:1 task)
PRE
PRACTICE
POST
Group 2 (continuous practice of 2:1 task)
PRE
PRACTICE
POST
In-phase trial
Anti-phase trial
2:1 trial
Break (10 min)

Fig. 2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B
Start
End
Post
0.09
0.06
0.03
0.00
Accuracy (*)
Variability (*)
0.16
0.12
0.08
0.04
Coherence
Intra left
Intra right
Inter (*)
Midline

Fig. 3

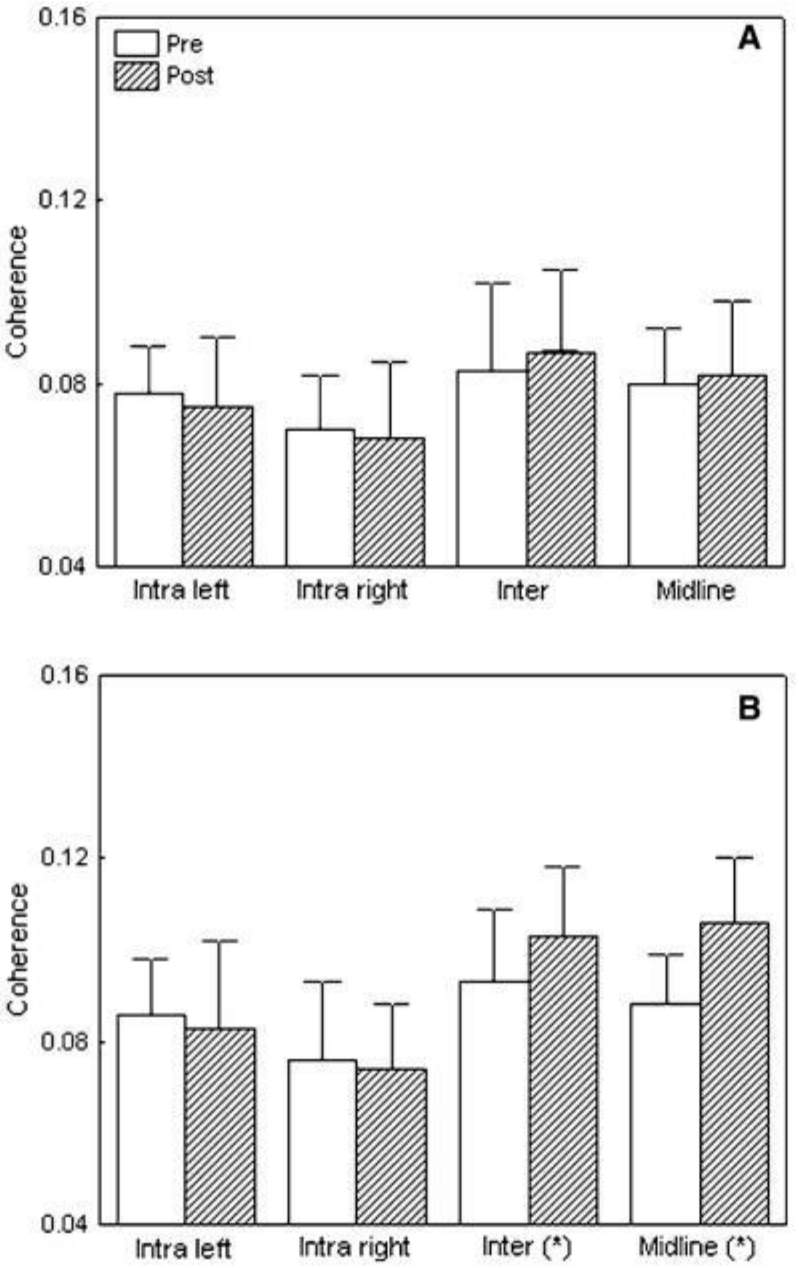

A
B
Pre
Post
Coherence
0.16
0.12
0.08
0.04
Intra left
Intra right
Inter
Midline
Inter (*)
Midline (*)

Fig. 4

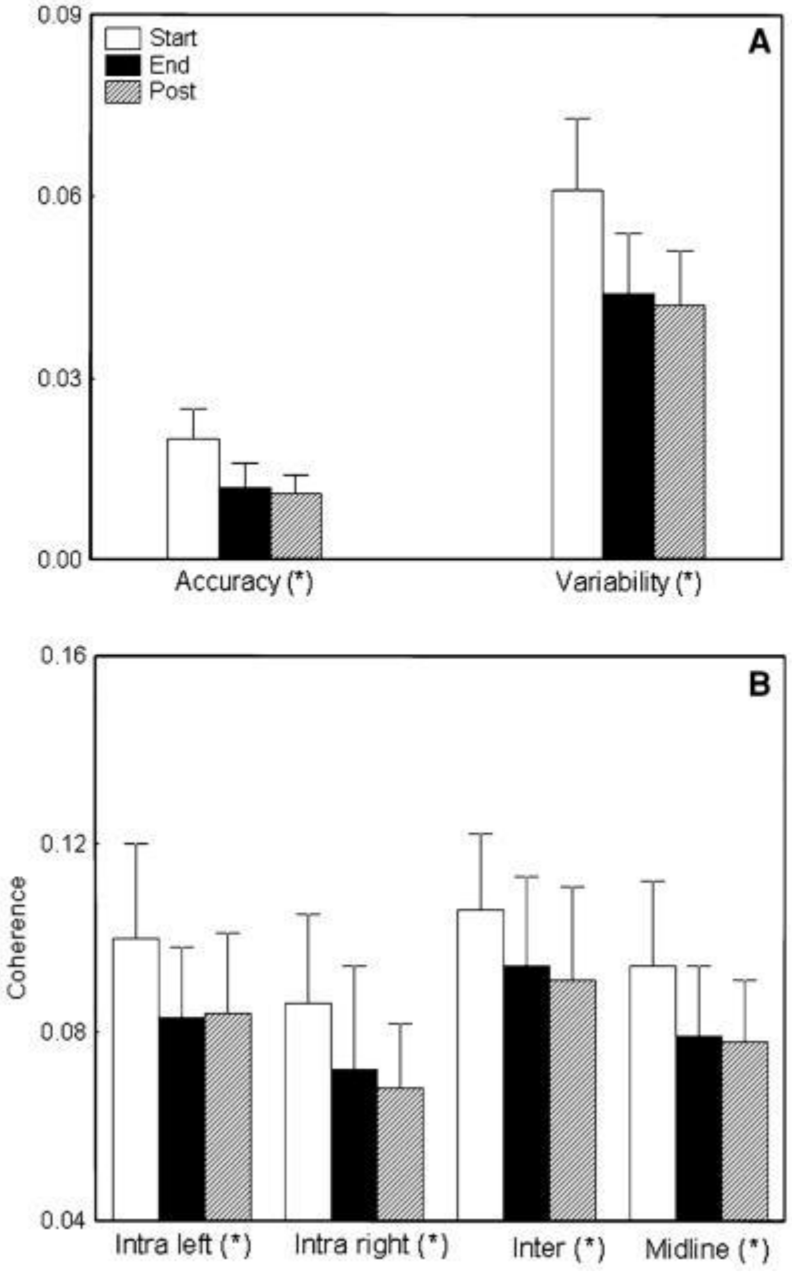

A
Start
End
Post
0.09
0.06
0.03
0.00
Accuracy (*)
Variability (*)
B
Coherence
0.16
0.12
0.08
0.04
Intra left (*)
Intra right (*)
Inter (*)
Midline (*)

Fig. 5

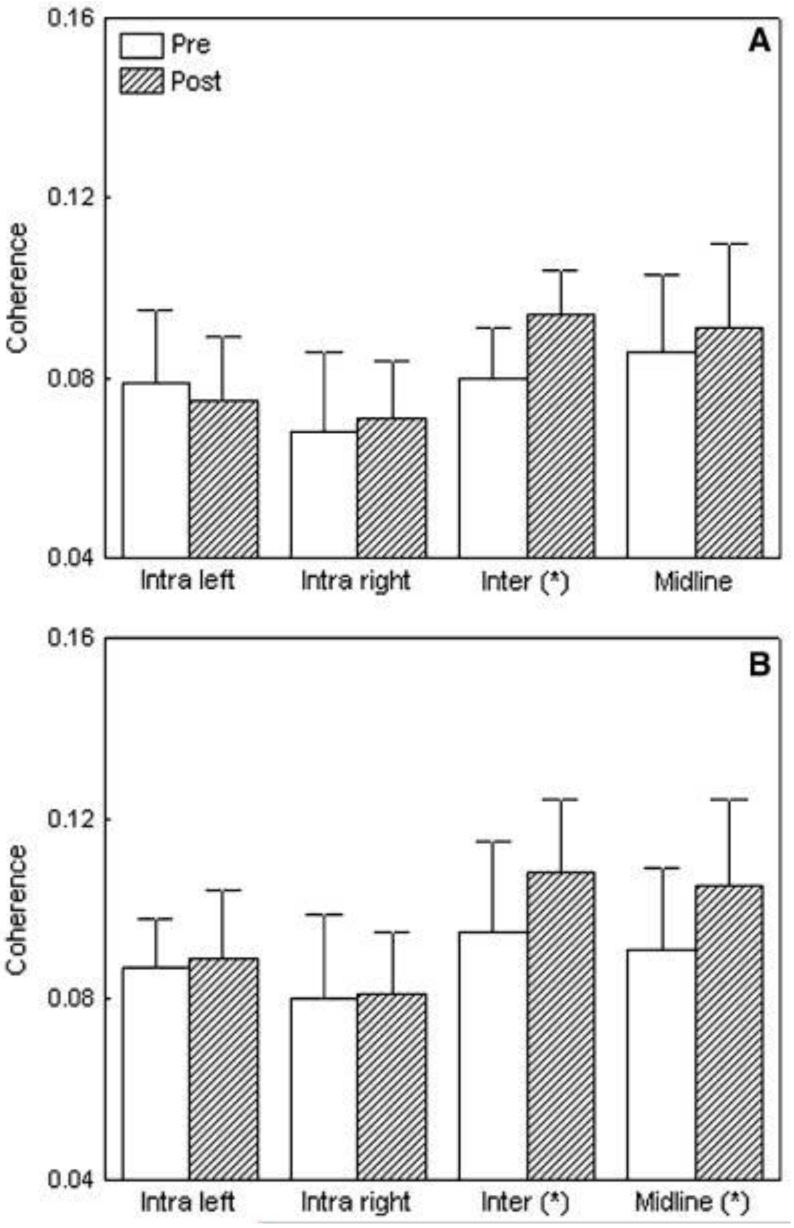
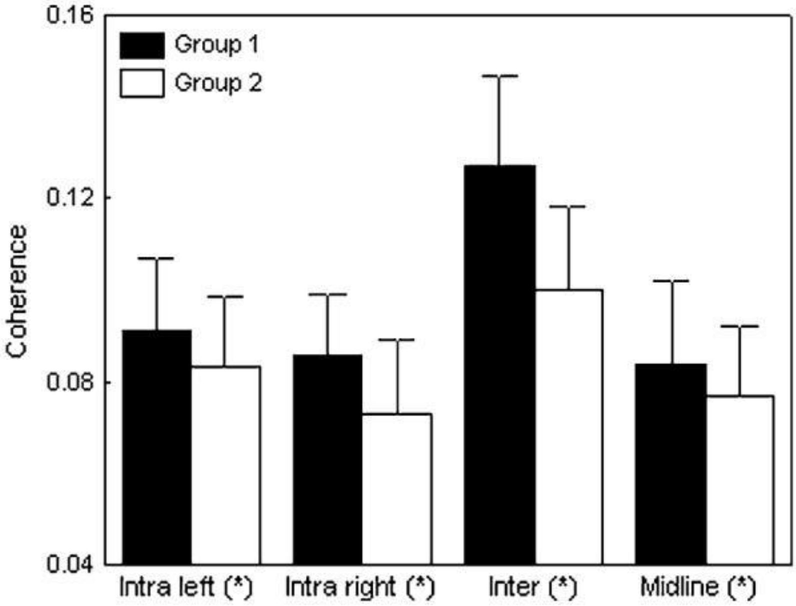

0.16
0.12
0.08
0.04
Coherence
Pre
Post
A
Intra left
Intra right
Inter (*)
Midline
0.16
0.12
0.08
0.04
Coherence
B
Intra left
Intra right
Inter (*)
Midline (*)

Fig. 6


0.16
0.12
0.08
0.04
Coherence
Group 1
Group 2
Intra left (*)
Intra right (*)
Inter (*)
Midline (*)