SHORT COMMUNICATION
Attentional demands reflect learning-induced alterations of bimanual coordination dynamics

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Abstract
This study aimed to investigate the effects of practice on bimanual coordination dynamics and attentional demands. Participants were asked to perform a dual-task associating a cyclic antiphase bimanual pattern and a discrete reaction time task. A pretest determined each individual critical transition frequency. In the training session, participants practised 120 trials. They were instructed to maintain the antiphase coordination pattern at the critical transition frequency. The training session was interrupted and followed by an intermediate test (after 60 trials) and a post-test (30 min after 120 trials), respectively. A retention test was performed 7 days after the end of the training session. Results showed that: (i) the number of transitions decreased as a consequence of practice; and (ii), subjects were able to maintain the antiphase pattern at a higher frequency than in the pretest. Analysis of the trade-off between relative phase variability and reaction time showed that participants were able to maintain a higher level of stability at the same (intermediate and post-test) or a lower attentional cost (retention test). These findings show that phase transition dynamics and pattern stability can be significantly modified as a result of practice. Changes in the trade-off between pattern stability and cost with learning confirm that the attentional cost incurred by the central nervous system to maintain pattern stability decreased with practice. In line with recent neurobiological studies, the present study provides new insights regarding relationships between brain processes, attentional demands and coordinated behaviour in learning bimanual patterns.

Introduction
The study of bimanual coordination dynamics has proved to be a useful tool by which to scrutinize the learning of new motor skills (e.g. Zanone & Kelso, 1992; Swinnen et al., 1997) and neural networks interactions (Swinnen, 2002). Moreover, the issue of attentional demands associated with learning a new interlimb coordination task is also of importance to connect cortical and behavioural dynamics and to explore the information processing activity of the nervous system in the control of coordinated behaviour (Jirsa et al., 1998). However, studies on interlimb coordination dynamics have rarely addressed the question of attention (for a review, see Monno et al., 2002). This paper addresses the issue of bimanual coordination flexibility by investigating how learning alters the stability of bimanual coordination. Moreover, it tackles the issue of the attentional demands associated with a change of coordination dynamics with learning.

Bimanual coordination is characterized by two preferred patterns, in-phase and antiphase (Kelso, 1984). The in-phase pattern proves to be more stable than the antiphase pattern, and an unavoidable switch from the latter to the former (a phase transition) occurs when oscillation frequency increases beyond a given critical threshold (Kelso, 1984). This entire behavioural picture was formalized by Haken et al. (1985) (the HKB model) through the dynamics of the relative phase between the components. Therefore, bimanual coordination is said to be governed by the spontaneous dynamics of relative phase. However, constraints imposed by spontaneous coordination dynamics on the actual behaviour do not preclude flexibility. Several studies have shown that subjects can permanently stabilize a novel coordination pattern with learning (Zanone & Kelso, 1992; Swinnen et al., 1997). It has also been shown that subjects can momentarily stabilize an existing preferred coordination pattern (Temprado et al., 1999) and then change the spontaneous bimanual coordination dynamics (Lee et al., 1996; Monno et al., 2000). However, the question arises of whether the coordination dynamics can accommodate influence to the additional task by further stabilizing the antiphase pattern and then, durably changing the dynamics of phase transition. The issue of the attentional demands associated to such a change of coordination dynamics with learning must also be addressed. Indeed, it has long been argued that the acquisition of complex skill over practice is paralleled by a change in the amount of information that can be processed simultaneously at a central level (Fitts & Posner, 1967; Shiffrin & Schneider, 1977).
Neurobiological studies using rhythmic auditory–motor coordination tasks have shown that the less stable (i.e., more difficult) syncopation pattern was associated with a greater activation of sensorimotor areas in the brain than the more stable synchronization pattern (Mayville et al., 1999, 2001). It has been hypothesized that such differences in neural ensemble activation mediate attentional demands associated with performing preferred coordination patterns. Behavioural studies have demonstrated that bimanual pattern stability and attentional demands strongly covary; the most stable pattern is also the less ‘expensive’ to perform for the central nervous system (CNS) and vice versa (Temprado et al., 1999; Monno et al., 2000; Zanone et al., 2001; for a review, Monno et al., 2002). In these studies, a dual-task paradigm involving a cyclic bimanual coordination task and a discrete reaction time (RT) task was used to investigate the interplay between attentional processing activity and bimanual coordination dynamics. The RT task was used as a probe to evaluate the central processing activity needed to maintain a coordination pattern at a given level of stability. The assessment of the attentional demands (RT and/or the difference in RT) through the dual-task paradigm proved to be a fairly direct and reliable evaluation of the activity devoted by the central processing mechanisms to perform bimanual coordination patterns.

The present experiment expands on previous studies in that it investigates the effects of practice on the dynamics of phase transition and antiphase pattern stability. In a recent study using magnetoencephalograph (MEG) signals and a syncopation-synchronization task to a metronome, Jantzen et al. (2001) described changes in the dynamics of cortical activity correlated with the increase in stability of the syncopation mode of coordination induced by learning. Initially, reduced power of MEG signals was observed in synchronization as compared to syncopation, consistent with putatively higher task demands associated with the latter (Boiten et al., 1992). By contrast, after training power differences were reduced or eliminated, suggesting that at the cortical level syncopation became more similar to synchronization. Such a change in the central processing activity could be associated to a decrease in the attentional demands imposed by syncopation (Boiten et al., 1992; Dujardin et al., 1993). To corroborate this hypothesis, the present study investigated the (co)evolution of bimanual coordination dynamics and attentional demands with learning. This question was addressed through the use of a dual-task paradigm consisting of a bimanual coordination pattern (antiphase) and a RT task. The main idea was to use behavioural probes to map the stability of the antiphase pattern at multiple movement rates both before and after learning. According to the results of Jantzen et al. (2001), we expected to observe: (i) a change in phase transition dynamics over practice, resulting from an increase in stability of the antiphase pattern; and (ii), a reduction of central processing demand incurred by the CNS to maintain the antiphase pattern.

Materials and methods

The experiment was undertaken with the understanding and written consent of each participant. Five participants manipulated a pair of customized joysticks to perform a dual task associating a bimanual coordination task and a RT task. In a trial, participants had to execute an antiphase pattern (assigned to a 180° relative phase), in which non-homologous muscles (pronation–supination) were activated simultaneously. For the RT task, participants were instructed to depress both buttons simultaneously with their feet as soon as possible after the onset of the auditory cue.

Results

Effects of practice on transition variables and antiphase pattern stability

First, we assessed the learning effects of practice captured through the change in maximum oscillation frequency, critical frequency (transition frequency) and the percentage of phase transition. We observed an increase in critical frequency, after the first block of 60 trials, for all the participants. Results also showed that the maximum frequency

Pretest

Participants performed a pretest involving a dual-task scanning procedure with four different frequencies (1.5, 2.0, 2.5 and 3 Hz). The pretesting session aimed to determine the individual critical level of transition frequency, i.e. the first frequency value for which a transition occurred for at least 50% of the number of trials performed by participants. After following the metronome for 15 s, participants depressed the buttons to stop the metronome, and then kept going on their own at the same frequency for 20 s. For each frequency condition, participants were instructed to share attention between the two tasks and to do their best in both tasks, that is to maintain a ‘maximum’ performance level. For each RT trials, 4–6 beeps were presented randomly. Twelve trials were performed for each level of frequency. After three trials, the performed oscillation frequency, the average relative phase and SD and the mean RT was returned as knowledge of performance to the participants and performance trade-off was assessed.

Training session

The learning procedure entailed 120 trials performed at the critical oscillation frequency. Participants were instructed to direct their attention to the bimanual coordination task to maintain the antiphase pattern. During the training session feedback was given to the subjects after each trials about: (i) the performed oscillation frequency; (ii) the average relative phase and SD; and (iii), the mean RT.

Intermediate test, post-test and retention test

An intermediate test was performed 5 min after a first block of 60 consecutive trials at the critical transition frequency identified in the pretest scanning procedure. The intermediate test consisted of the same scanning procedure as that used in the pretest. Then, a new maximum oscillation frequency and a new transition frequency level were eventually determined. The maximum oscillation frequency was the frequency at which 100% of the phase transition was observed. The new value of critical frequency was used to train the participants in the second block of 60 trials of the training session. Thirty minutes and 7 days after the end of the training period, participants performed a post-test and a retention test, respectively, with the same scanning procedure as in the pretest and the intermediate test (1.5, 2.0, 2.5, 3.0 Hz or more if possible).

For each trial, we computed the average point-estimate relative phase and the associated SD, which assesses the central tendency of the coordination pattern and its stability, respectively (see Zanone & Kelso, 1997, for a complete discussion). Four dependent measures were considered to analyse the results obtained in the different tests: (i) the maximum oscillation frequency performed by the participants; (ii) the percentage of phase transition (%); (iii) the SD of the relative phase (); and (iv), the RT (in ms) as the time interval between the onset of the auditory signal and the moment at which the first trigger button was depressed.

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increased from the pretest (3.0 Hz) to the post-test and the retention test (3.5 Hz) for all the participants. Thus, the practice session resulted in an increase in the capability of performing the antiphase pattern above a level at which, prior to practice, it would typically switch to in-phase.

We carried out a 4 (test) × 4 (frequency) analysis of variance (ANOVA) with repeated measures on both factors on the mean percentage of phase transition observed for each level of oscillation frequency. Results showed a significant effect of test ($F_{3,12} = 21.72$, $P < 0.001$), frequency ($F_{3,12} = 10.10$, $P < 0.001$) and for the interaction between test and frequency ($F_{9,36} = 5.66$, $P < 0.001$). Post hoc Newman-Keuls analysis showed a decrease in the number of phase transitions in the intermediate, post-test and retention test for all frequency levels except 1.5 Hz (Fig. 1). Moreover, the number of phase transitions was equivalent in the intermediate test, the post-test and the retention test excepted at 3.0 Hz. At this frequency, a decrease of the number of phase transitions was observed from the intermediate test to the retention test and from the post-test to the retention test. In the pretest, increasing oscillation frequency led to an increase of the number of phase transitions. In the intermediate test, increasing oscillation frequency led to an increase of the number of phase transitions only from 1.5 Hz to 3.0. In the post-test and the retention test, the number of phase transitions was equivalent for all frequencies. As a consequence, the critical 50% transition threshold was reached at 2.0 Hz in the pretest and at 3.5 Hz in the post-test and the retention test.

A 4 × 4 (test × frequency) ANOVA was carried out on the SD of the relative phase of the antiphase pattern (Fig. 2). This analysis revealed a significant effect of frequency ($F_{3,12} = 31.01$, $P < 0.001$) and for the interaction between frequency and test ($F_{9,36} = 4.22$, $P < 0.001$). Post hoc Newman-Keuls analysis showed that learning resulted in a decrease of SD of the relative phase for all the frequency levels except 3.0 Hz in the intermediate test, the post-test and in the retention test. At this frequency, relative phase variability was higher in the intermediate test, the post-test and the retention test than in the pretest. The SD of relative phase was equivalent in the pretest, the post-test and the retention test in the intermediate test. Increasing oscillation frequency resulted in an increase in relative phase variability for all frequencies excepted between 2.5 Hz and 3.0 Hz. In the intermediate test and the post-test, the SD of the relative phase increased from 1.5 Hz to 2.0 Hz and from 2.5 Hz to 3.0 Hz, though it was equivalent between 2.0 Hz and 2.5 Hz in the retention test, variability of the relative phase increased from 1.5 Hz to 2.5 Hz and to 3.0 Hz but it was equivalent between 1.5 Hz and 2.0 Hz.

**Effects of practice on attentional demands**

A 4 (test) × 4 (frequency) ANOVA was carried out on the RT (Fig. 3). This analysis revealed a significant effect of frequency ($F_{3,12} = 6.06$, $P < 0.001$) and for the interaction between frequency and test ($F_{9,36} = 2.09$, $P < 0.05$). Post hoc Newman-Keuls analysis showed that RT decreased for all the frequency levels except 3.0 Hz in retention test ($P < 0.05$). The RT was equivalent in the pretest, the intermediate test and the post-test for all the frequency levels except 1.5 Hz. In the retention test, RT increased from 2 Hz to 2.5 Hz and to 3.0 Hz and from 2.5 Hz to 3.0 Hz. In the post- and the retention tests, participants were able to perform the antiphase pattern at 3.5 Hz. At this frequency, the mean RT was very close to the values observed at 3.0 Hz (439 ms and 427 ms, respectively).

**Discussion**

The present study investigated two main issues: (i) has practice any learning effects on transition variables and on antiphase pattern stability; and (ii), are these effects (if they exist) associated with a change in the attentional demands? The results show that transition variables can be significantly modified as a result of practice. Moderate training at the transition frequency led to an increase in both critical and maximum oscillation frequency. Moreover, a decrease in the percentage of phase transition was observed in the different tests as a result of practice. The effect of practice on the number of phase transition was even observed at 3.5 Hz, suggesting that learning effects spontaneously transferred to nonpracticed frequencies. Results also show that, as a consequence of practice, participants become less sensitive to oscillation frequency, and thereby improved the range of their bimanual performance. The decrease in the percentage of phase transitions was consistent partly with a decrease in relative phase variability. Indeed, at low and moderate oscillation frequency levels (1.5, 2.0 and 2.5 Hz), the decrease in the percentage of phase transition was paralleled by an increase in antiphase pattern stability. By contrast, at high frequency levels (3.0 and 3.5 Hz), relative phase variability was equivalent or higher in the intermediate test, the post-test and the retention test,
through the number of phase transitions decreased. This result suggests that changes of phase transition are not a direct consequence of change in the stability of the antiphase pattern. In a previous study, we have shown that phase transitions can be also constrained by central (attentional) processing demands associated with sustaining the antiphase bimanual pattern (see below for confirming evidence).

Overall, the results observed for transition variables and pattern stability corroborate those obtained by Jantzen et al. (2001) in a synchronization-syncopation task.

The comparison of the RTs before and after practice strongly suggests any change in the dynamics of phase transitions was accompanied by corresponding changes in attentional demands. By contrast, in the intermediate test and the post-test, relative phase variability increased and RT remained equivalent. Such a change in the trade-off between pattern stability and attentional cost is informative. It suggests that with practice, participants became able to maintain a higher level of stability of the bimanual pattern at a lower attentional cost. On the other hand, the covariation of relative phase variability and mean RT was only observed in the retention test. This result shows that pattern stability and attentional processes do not necessarily change at the same rate. The delayed decrease of attentional cost suggests the existence of consolidation processes that occur between sessions and overnight (Brashers-Krug et al., 1996; Shadmehr & Brashers-Krug, 1997; Shadmehr & Holcomb, 1997). Results also show that at 3.0 Hz and 3.5 Hz, though relative phase variability continued to increase, RT roughly stabilized. This suggests that attentional demands associated with performing the antiphase pattern may act on the (non) occurrence of phase transition, at least at high frequency levels (see also Monno et al., 2000).

The change in attentional demands associated with the increase of stability of the antiphase pattern corroborates the results obtained in neurophysiological studies describing neural correlates of the stability and change of behavioural coordination using high density SQUID (Jantzen et al., 2001), electroencephalogram arrays (Kelso et al., 1992; Mayville et al., 1999, 2001) as well as functional magnetic resonance imaging (Fuchs et al., 2000). Jantzen et al. (2001) concluded that training altered the way in which the brain performs the task. Specifically, they showed that desynchronization of oscillatory activity of the neural ensembles of the cerebral cortex is an appropriate measure of learning. The study of Jantzen et al. (2001) also led to the hypothesis that the post-training CNS activity differences reflect a decrease in

the associated attentional demands imposed by syncopation pattern. Thus, the authors’ conclusion was that learning and attention are co-implicative and may involve changes in cell body/synaptic coupling. The results of the present study corroborate this hypothesis using appropriate measure of attentional processing demands. However, in their study, Jantzen et al. (2001) did not use a retention test, thereby questioning whether the effects of practice were permanent over some time period; that is, whether change in cortical activity observed following training continued to evolve over days. In the present study, the reduction of attentional demands was only observed in the retention test, suggesting a delayed effect of training on the RT measure of attentional demands. Thus, an interesting issue for further studies would be to couple brain imaging and dual-task experiments to assess online (parallel) and delayed evolution of cortical activity and attentional demands with learning.

Abbreviations

ANOVA, analysis of variance; CNS, central nervous system; MEG, magnetoencephalograph; RT, reaction time.

References


