Perceptual and motor contributions to bimanual coordination

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Received 24 September 2003; received in revised form 23 March 2004; accepted 23 March 2004

Abstract

Following earlier work by Mechsner et al. (Nature 414 (2001) 69), the purpose of this experiment was to determine the perceptual and motoric contributions to bimanual coordination. Twenty right-handed, healthy, young adults performed continuous, horizontal, linear movements of both upper limbs at frequencies of 1.5 and 2.0 Hz. The goal was to control the spatial-temporal displacement of two flags by coordinating upper limb movements in two perceptual conditions. In a congruent condition, the movement of the flags matched the movement of the upper limbs. In an incongruent condition, the movement of the flags was opposite to the movement of the upper limbs. Measures of error in coordination provided support primarily for a motor view of bimanual coordination, and failed to replicate the earlier findings of Mechsner et al.

The bimanual coordination literature has revealed that certain spatial-temporal patterns of movement are generated and maintained more easily than other patterns. In general, these preferred patterns fall under two principles: an egocentric principle, that constrains movements made in mirror symmetry using similar muscle groups, and an allocentric principle, that constrains movements made in the same direction [12]. For upper limb movements made in the horizontal plane, these principles of coordination are realized in two stable patterns: in-phase (0° relative phase) and anti-phase (180° relative phase) [7,8,11,17]. In-phase coordination refers to mirror-symmetrical movements made simultaneously towards and away from the longitudinal axis of the body, whereas anti-phase coordination refers to movements made in the same direction, simultaneously, from one side of the longitudinal axis of the body to the other.

The relative stability of in-phase and anti-phase coordination becomes apparent when individuals perform the patterns at frequencies that are faster than preferred [8], when they attempt to switch from one pattern to another [3, 10], or when they try to learn a new coordination pattern [6, 19]. With increasing movement frequency, in-phase coordination remains stable while anti-phase coordination destabilizes, and if unopposed, eventually results in an involuntary transition to in-phase coordination [2,8]. Involuntary transitions from in-phase to anti-phase coordination are rare [8]. The greater stability of in-phase coordination makes voluntary transitions from in-phase to anti-phase coordination more difficult (as measured by longer switch times) than voluntary transitions in the reverse direction [3,10]. Due to the stability of in-phase and anti-phase coordination, intermediate patterns are difficult to perform and require extensive practice to learn [6,19].

Currently, there exists a controversy in the literature as to why in-phase and anti-phase coordination are inherently more stable than other phase relations in horizontal upper limb movements. The motoric view suggests that in-phase performance is the more stable bimanual coordination pattern because homologous muscle groups are activated simultaneously [4,8,13]. Anti-phase performance is more variable than in-phase coordination because non-homologous muscle groups are activated simultaneously [4,8,13].

Mechsner et al. [9] recently challenged the motoric view of bimanual coordination and proposed that many of the
observed characteristics of bimanual coordination are perceptual in nature rather than due to motoric contributions. One origin of this perceptual view was research showing that rhythmically moving in-phase stimuli were perceived to be more stable than rhythmically moving anti-phase stimuli [18]. That is, the visual perception of the phase relationship between two objects may play a fundamental role in the stability of interlimb coordination [18]. A perceptual view contends that the constraints imposed on coordination as suggested by the egocentric and allocentric principles are not based specifically on limb movements per se, but rather on the perceptual consequences that accompany these movements. In terms of upper limb coordination in the horizontal plane, in-phase coordination is the more stable of the two coordination patterns because it is perceived to be mirror symmetrical, whereas anti-phase coordination is more variable because it is perceived to be asymmetrical.

Mechsner et al. [9] provided additional support for the perceptual view of bimanual coordination in a series of experiments with healthy young adults. Three experimental paradigms were used: a finger oscillation task, a bimanual finger-tapping task and a bimanual circle drawing task, in which the goal for each task was visually defined. In all experiments it was found that, regardless of the movements of the effectors, performance was most stable when movements were visually in-phase. Increases in movement frequency resulted in spontaneous transitions from movements that were visually anti-phase to visually in-phase. Based on these results and related findings under other experimental manipulations, Mechsner et al. [9] concluded that the perceptual qualities of the movement dominated the motoric constraints.

A few methodological issues associated with the experiments conducted by Mechsner et al. [9] suggest that further investigation is warranted. One issue was that the bimanual circle drawing task in Experiment 3 was internally paced, resulting in considerable variation in movement frequency between participants, coordination patterns and visual-motor congruency. In an attempt to improve stability and accuracy of movements that were visually in-phase, participants may have performed this pattern at a slower movement frequency. Although it may have appeared that visually in-phase movements were more stable than visually anti-phase movements, the possibility exists that speed was being traded for accuracy in the incongruent visual-motor conditions. Another potential factor that could have introduced a divergence with research supporting a motoric view of bimanual coordination was the nature of the task. For a bimanual circle-drawing task, movements always continue in the same direction; there are no movement reversals. Compared to other bimanual coordination tasks in which the effectors must stop and reverse direction [8], bimanual circling may under-represent the contribution of proprioceptive sources of information. If this difference in the nature of intrinsic feedback has a critical impact on coordination performance, it may well be the case that bimanual circle drawing enhances the importance of visual feedback information, because of the reduced importance or input from proprioceptive sources. In general, despite these methodological questions, the perceptual view can be seen as a legitimate challenge to the motoric basis of bimanual coordination. The perceptual view was supported by research conducted with healthy young adults and specific experimental paradigms [9]. However, it is unknown whether the perceptual view can be extended to a different experimental task. Specifically, the impetus for the present experiment was to determine whether the perceptual view would be supported with a motor task that provided considerably more proprioceptive feedback than the one used by Mechsner et al. [9].

Twenty (10 female, 10 male) healthy, right-handed young adults served as participants (mean (M) age = 19.5 years, range = 19–23 years). All participants read and signed a consent form prior to testing and received an honorarium of CAD$10.00 for their participation. This experiment received ethical approval from the Research Ethics Board at McMaster University prior to being conducted.

The goal of the task was to coordinate the movement of two flags in visual in-phase or visual anti-phase by continuously moving two slide carriages linearly and horizontally with the upper limbs. To move the slide carriages, participants grasped vertically moulded handgrips that were bolted to each slide carriage. Participants sat on a height-adjustable, non-swivel chair with their body midline positioned at the centre of the apparatus and with elbows bent at 90 degrees.

The slide carriages and the participants’ hands were hidden from view by a horizontal wood platform that was placed 18 cm above the slide carriages (see Fig. 1). In order to prevent visual feedback from the upper limbs a cloth bib extended from the proximal edge of the wood platform and was secured with safety pins behind the participant’s neck. The cloth bib did not interfere with the movements of the upper limbs.

Two fluorescent yellow flags (2 cm wide, 10 cm high) were attached to the left or right slide carriage and extended 1 cm beyond the distal edge of the wood platform.

Fig. 1. Illustration of apparatus. Participant is wearing a cloth bib to block vision of the upper limbs. White flag indicates set up for the incompatible condition.
Participants were told that the goal of the task was to continuously move each yellow flag back and forth within a 16 cm region. The boundaries of the region were clearly marked. In the congruent condition, the left and right flag attached directly to the left and right slide carriage, respectively. Therefore, in these visual-motor congruent-conditions the visual information provided by the movements of the flags matched the movements of the upper limbs (i.e., visual in-phase corresponded with muscular in-phase and visual anti-phase corresponded with muscular anti-phase) (see Fig. 2). In the incongruent conditions, the left flag attached directly to the left slide carriage while the right flag extended from a chain and pulley system that was attached to the right slide carriage (see flag attached to dotted line in Fig. 1). Therefore, the movement of the left flag matched the movement of the left upper limb but the movement of the right flag was transformed by 180° to the right upper limb. By this arrangement, anti-phase limb movements corresponded with in-phase motions of the flags, and in-phase limb movements corresponded with anti-phase motions of the flags (Fig. 2).

Participants were instructed to coordinate the flags in an in-phase or anti-phase pattern. No reference was made to the movements of the upper limbs or to the 180° transformation between the right flag and right upper limb. Visual in-phase was performed by simultaneously moving the left and right flags away from and then toward the midline of the body. Visual anti-phase was performed by moving the left flag toward while moving the right flag away from the midline of the body, and vice versa. Instructions on how to perform the two coordination patterns were described verbally using a standard set of instructions and through demonstration by the examiner using two model flags. Participants were instructed to move the flags in a rhythmic and fluid manner without stopping, to maintain the pace with a metronome beat, to keep the flags within the amplitude boundaries, and to ‘stay’ with the coordination pattern in which they started throughout the trial. If participants made an involuntary transition away from the intended pattern they were to try and reacquire the original pattern.

Participants practiced coordinating the flags at a self-paced frequency until they were able to perform the requested pattern within 15° of the intended phase relationship (less than 5 min of practice). Participants then practiced one trial at 1.0 Hz to familiarize themselves with the task (paced by an auditory metronome). The experimental trials were performed at 1.5 Hz and 2.0 Hz. Participants performed 16 incongruent trials and 16 congruent trials. Half the participants performed the congruent condition followed by the incongruent condition while the other half performed in the reverse order. Within each congruency condition, visual in-phase and visual anti-phase trials were counterbalanced and a 2.0 Hz trial always followed a 1.5 Hz trial for the same coordination pattern. This counterbalancing resulted in four trials for each coordination pattern at each frequency and for each congruency condition. The length of each trial was 20 s and the inter-trial interval was approximately 20 s.

Data were transferred offline for analysis. Relative phase between the movement of the hands was used to measure interlimb coordination. In the congruent condition, visual/muscular in-phase and visual/muscular anti-phase coordination corresponded with limb relative phase measures of 0° and 180°, respectively. In the incongruent condition, visual in-phase/muscular anti-phase and visual anti-phase/muscular in-phase corresponded with limb relative phase measures of 180° and 0°, respectively. In the interest of consistency, all results are reported with respect to upper limb coordination movements.

Overall performance error of relative phase was measured using root mean square error (RMSE), calculated using the formula \( \text{RMSE} = \sqrt{\text{standard deviation of relative phase}^2 + \text{absolute mean error of relative phase}^2} \).

The more accurate and more stable the performance the lower the RMSE. Movement frequency and amplitude were also measured. Involuntary phase transitions were identified as the point at which relative phase first deviated from the intended pattern by more than ±30° (which is approximately equivalent to twice the standard deviation under most of the anti-phase conditions examined in Experiment 1 in [16]) for a minimum of 2 s.

Statistical analyses were performed using a mixed-design ANOVA with order of presentation of the congruency conditions (incongruent-congruent, congruent-incongruent) as the between-group factor and all other variables as within-group factors. RMSE was analysed with a 2 Congruency Condition (congruent, incongruent) \( \times 2 \) Phase (muscular in-phase, muscular anti-phase) \( \times 2 \) Frequency (1.5, 2.0 Hz) ANOVA. Frequency and amplitude of movement was analysed using a 2 Congruency Condition (congruent, incongruent) \( \times 2 \) Phase (muscular in-phase, muscular anti-phase) \( \times 2 \) Frequency (1.5, 2.0 Hz) ANOVA.

Analyses of overall relative phase performance error (RMSE) revealed significant main effects for Condition \( F_{1,18} = 31.00, \ P < 0.05 \), Phase \( F_{1,18} = 107.83, \ P < 0.05 \), and Frequency \( F_{1,18} = 23.95, \ P < 0.05 \). Significantly greater performance error was associated with the
involving the order factors. All three measures of relative phase failed (both metronome frequencies (1.5 Hz muscular in-phase was performed with equivalent error for muscular anti-phase performance deteriorated (performed with equivalent RMSE. At the higher frequency compared to muscular anti-phase (M = 13.5 cm), and during the 1.5 Hz (13.9 cm) compared to the 2.0 Hz (13.6 cm) frequency. An interaction between Phase and Frequency [F_{1,18} = 4.50, P < 0.05] indicated that the largest amplitude was produced during muscular in-phase coordination at the 1.5 Hz movement frequency and the smallest amplitude was produced during muscular anti-phase coordination at the 2.0 Hz movement frequency.

Analyses of the observed movement frequencies revealed main effects for Condition [F_{1,18} = 12.61, P < 0.05] and Phase [F_{1,18} = 19.6, P < 0.05] indicating that more accurately performed movement frequencies were achieved in the more stable coordination pattern and the congruent condition. Overall, the congruent condition was performed at a significantly higher frequency than the incongruent condition (M = 1.9 and 1.5 Hz, respectively) and muscular in-phase (M = 1.9 Hz) was performed at a significantly higher frequency than muscular anti-phase coordination (M = 1.5 Hz, respectively). Two-factor interactions were found for Condition \times Phase [F_{1,18} = 18.07, P < 0.05], Condition \times Frequency [F_{1,18} = 10.78, P < 0.05] and Phase \times Frequency [F_{1,18} = 27.32, P < 0.05]. Because a significant three-factor interaction between Condition, Phase and Frequency [F_{1,18} = 11.35, P < 0.05] was also observed only the latter effect will be described. Post hoc comparisons revealed that participants were able to perform muscular in-phase at the requested frequencies during both congruency conditions but were only able to perform muscular anti-phase at the requested frequency for the congruent condition at 1.5 Hz. For the 2.0 Hz congruent condition, and for both metronome frequencies for the incongruent condition, participants were significantly slower than the target metronome pace during anti-phase coordination. Lastly, it should be noted that in none of the trials was the criterion met for an involuntary transition, likely because the participants had been specifically instructed to remain in the original pattern and to regain that pattern if it became destabilized.

The purpose of this experiment was to determine the contributions of motoric and perceptual factors in the performance of bimanual coordination patterns [4,8,9,13]. Based on recent evidence [9] we asked whether in-phase coordination is more stable than anti-phase coordination because homologous muscle groups are activated simultaneously or because the movement is visually perceived to be mirror symmetrical?

The results primarily supported the motoric view of bimanual coordination. Measures of RMSE revealed that in-phase coordination of the upper limbs was performed with
significantly greater accuracy and stability than anti-phase coordination, regardless of the visual-motor congruency conditions. Moreover, in-phase coordination of the upper limbs was unperturbed by anti-phase visual information, a finding that directly contradicts the findings of Mechsner et al. [9] but which supports the conclusions of Bogaerts et al. [1]. The observed amplitude and frequency data also support the motoric view of bimanual coordination. Overall, participants produced amplitudes and frequencies that were significantly less than the target goals during muscular anti-phase coordination at 2.0 Hz. The results suggest that deterioration in performance stability and accuracy was associated with a decreased ability to perform at the target amplitude and frequency.

Although the current results mainly lend support to the motoric view, there was some evidence to suggest that the perceptual information influenced motor control. Anti-phase coordination of the upper limbs became less accurate when provided in-phase visual feedback (during incongruent conditions). One possibility for this deterioration is because anti-phase coordination is inherently less stable than in-phase coordination, it is more susceptible to destabilization by other factors than an in-phase pattern. An alternative possibility is that the visual symmetry from the motions of the flags may have a stronger influence on motor coordination in general than does an asymmetric visual flag motion. If so, then it would be the anti-phase motor pattern that would be affected most because of the strongest spatial incongruence effect. Previous studies [8, 10] have shown that limb coordination tends to destabilize prior to a phase transition. It is possible that muscular anti-phase was destabilized as a result of the attraction of the in-phase visual information. This finding provides some support for the influence of visual perception in bimanual coordination, specifically during anti-phase coordination with incongruent visual feedback [5].

Although the results do not support the perceptual view, they do lend credence to the suggestion that the concept of congruency should be incorporated into movement coordination theory. Previous research [5,14] (see ref. [15] for a review) and the current research suggest that coordination stability decreases as the congruency between perception and action is reduced. Therefore, congruency between the visual information provided by the environment and the movement of the upper limbs may be instrumental in determining the stability of motor behaviour.

We suggest that a likely reason why the present findings failed to replicate the findings of Mechsner et al. [9] is related to task specificity. For example, their finger oscillation task involved isolated abduction and adduction of the index fingers, which is motorically very challenging. In their bimanual circle-drawing task the perceived movement of the flags was dissociated from the movement of the upper limbs because the right flag moved at a higher frequency than the right hand. This was a complex task that took a considerable amount of practice to learn and consequently may not have examined the intrinsic coordination patterns per se. Therefore, there may be some task specificity associated with the findings that support the perceptual view of motor coordination.

Another task-related difference between the present experiment and the work of Mechsner et al. [9] was the availability of proprioceptive feedback. In the present study the friction of the slide apparatus and the reversal at the end of the movement amplitudes may have directed participants’ attention towards the proprioceptive feedback from the upper limbs. In contrast, the unidirectional, circle-drawing movements in the Mechsner et al. [9] study (Experiment 3), arguably, made the bimanual coordination actions much more dependent on visual feedback, again suggesting that the perceptual and motor determination of coordination may be task specific. The roles of information feedback in the determination of coordination performance, perhaps as a function of the performer’s intentions and the task demands, remains as an important question for future research.

Acknowledgements

This research represents part of the research conducted by the first author towards her MSc degree and was supported by a grant from the Ontario Ministry of Health awarded to the second author.

References


