Stabilizing bimanual coordination: Changes in interlimb interactions

de Boer, B.J.

2013

Summary

In rhythmical bimanual coordination, coordinative stability is determined by the coupling between the hands. When both hands move at the same relatively low frequency, two coordination patterns can be executed stably: in-phase coordination (i.e., mirror-symmetrical movements of the hands) and antiphase coordination (i.e., isodirectional movements of the hands). At higher frequencies only in-phase coordination can be performed stably. This difference in coordinative stability has been formally captured by the Haken-Kelso-Bunz model (HKB model), which consists of a pair of nonlinearly coupled nonlinear oscillators. Within this model, bimanual coordination is studied in terms of the relative phase between the oscillators (Φ) and its variability, which provides an index of coordinative stability. The HKB model captures the stable execution of in-phase (Φ = 0°) and antiphase coordination (Φ = 180°), as well as the essential role of movement frequency: when movement increases, coordinative stability of antiphase coordination decreases, culminating in a transition to in-phase coordination at a critical frequency. Extensions of this model were successful in accounting for influences of additional factors such as the difference between uncoupled frequencies of the moving limbs and handedness. Because the HKB model does not provide information regarding possible underlying processes, subsequent studies have focused increasingly on the link between the model and underlying system properties and processes.

Considering that bimanual coordination is governed by the coupling between the hands, it is relevant to determine the contributions of the underlying sources of interlimb interaction to the stability of bimanual coordination. In the literature, various candidate sources of interlimb coupling have been proposed. Using an established methodology, the research reported in the present thesis focused on three functionally defined sources of interlimb interaction. First, *integrated timing* reflects interaction processes related to feedforward timing of the efferent signals that specify the intended bimanual coordination pattern, without consideration of potential adjustments based on afferent feedback. Second, *error correction* reflects the intentional correction of relative phasing errors based on kinesthetic afference, resulting in stabilization of the intended bimanual coordination pattern. Third, *phase entrainment* pertains to the unintentional entraining influences stemming from contralateral afference, leading to unintended attraction towards specific phase relations between the limbs. Changes in the stability properties of bimanual coordination that occur as a function of task-related parameters like movement frequency and amplitude, learning, and development, should be related

to changes in interlimb interactions. The research reported in the present thesis thus aimed to elucidate how changes in coordinative stability are engendered by changes in the interlimb interactions underlying coordinative stability. In particular, we focused on changes in coordinative stability and interlimb coupling at both short (viz. movement frequency and amplitude) and longer time scales (viz. learning and development). In Chapters 2, 4, and 5 all three sources of interlimb interaction were investigated, while in Chapter 3 only phase entrainment was studied.

In Chapter 2, the influence of movement frequency on coordinative stability was examined in terms of the three sources of interlimb interaction of interest. To this end, five tasks involving passive and active movements of the hands were systematically compared. In each of these tasks, the different sources of interaction were assumed to be involved to a different extent. First, during unimanual coordination with a pacing signal (task UN) no sources of interlimb interaction were present. Second, for unimanual coordination in the presence of phase-shifted passive movements of the contralateral hand (task UNm), the active hand was entrained towards in-phase and antiphase coordination with the passively moving hand. Hence, comparison of UNm and UN served to tease apart the contribution of phase entrainment. Furthermore, when the actively moving hand tracked the passive movements of the contralateral hand, either in the presence of an auditory distracting signal (task KTa) or without such a signal (task KT), the coordination pattern between the hands was stabilized by interactions associated with error correction. Whereas interactions due to phase entrainment were present in both KTa and UNm interlimb, error correction was present in KTa but not in UNm. Hence, the influence of error correction could be assessed by comparing KTa to UNm. In addition, the robustness of the error correction process was examined by comparing KT and KTa, because this comparison revealed its susceptibility to the distracting influences of the auditory signal. Finally, during active bimanual coordination (task AB), participants executed active movements of both hands in a specified pattern, implying that in this task coordinative stability was also enhanced by integrated timing of the bimanual control signals. The contribution of integrated timing was assessed by comparing AB to KT, because in KT only phase entrainment and error correction were involved while AB involved all three sources of interaction. Finally, integrated timing was also assessed by comparing AB to UNm, because error corrections were found to be hardly involved in AB.

The effect of movement frequency was studied by systematic pairwise comparisons of the five tasks for three different frequencies for in-phase and antiphase coordination. The highest frequency was equal to the critical frequency of each participant, i.e., the frequency at which the stability of antiphase coordination was lost. Results confirmed that bimanual coordination was stabilized by each of the three sources of interlimb interaction, with the differential stability of in-phase and antiphase coordination resulting predominantly from interactions associated with integrated timing. Moreover, at low frequencies integrated timing seemed sufficient to stabilize bimanual coordination, whereas a shift towards a more prominent role of error correction was observed at higher frequencies for the more difficult antiphase pattern. These results suggested that for low frequencies coordinative stability was mainly achieved by means of open-loop control of the bimanual pattern, whereas at the critical frequency stabilization of the pattern required a shift to closed-loop control in which relative phase errors were corrected based on kinesthetic afferent information. The contribution of phase entrainment was not influenced by movement frequency. Furthermore, the observation that also kinesthetic tracking involved coordinated bimanual muscle activity indicated that error corrections were more effective when bimanual control signals were generated. Presumably, in this manner a bimanual reference frame was generated that allowed for sensory predictions against which the actual kinesthetic afference could be compared.

Because both empirical results and theoretical considerations have suggested that larger movement amplitudes may induce stronger phase entrainment, this relation was scrutinized in Chapter 3. The central question was whether phase entrainment strength was influenced by movement amplitude as such or by the amplitude relation between the hands. For this purpose, a previously published dataset was re-analyzed and compared to the results of a new experiment. In both experiments, phase entrainment strength was determined by comparing the coordination of unimanual movements with a pacing signal (task UN) to the performance of the same task in the presence of distracting passive movements of the contralateral hand (task UNm). In the first experiment two amplitudes of the passive hand movements were imposed without having any restrictions on the amplitude of the actively moving hand. Since the active hand moved at the same amplitude in the two amplitude conditions, the amplitude relation between the hands was different in the two conditions. Specifically, the amplitude relation between the passive and active hand was 1:1.9 for the small amplitude and 1:1 for the large amplitude. In the second experiment the same movement amplitudes of the passively moving hand were used, but the amplitude relation was 1:1 between the two hands in both amplitude conditions. The results indicated that phase entrainment strength was only influenced by a change in the amplitude relation between the limbs (as obtained for Experiment 1) and not by amplitude as such (Experiment 2). These results suggested that entrainment to the contralateral hand was not only influenced by the strength of afferent signals, but also by the susceptibility of the active hand movements to external influences.

In Chapter 4 the effect of learning a new coordination pattern on the underlying interlimb interactions was examined, thereby assessing the changes in interlimb interactions at a longer time scale. Participants learned to execute a new bimanual coordination pattern (Φ = 90°) and changes in bimanual coordination were related to changes in the underlying contributions of integrated timing, error correction, and phase entrainment. For this purpose, participants executed the four tasks that involved the three interlimb interactions to a different extent, i.e., tasks AB, KT, UNm, and UN. Learning effects were assessed for in-phase and antiphase coordination, the practiced 90° pattern, and its mirror-symmetrical transfer pattern (Φ = 270°). In addition, bimanual performance and changes in the sources of interlimb interaction were compared for learning with an internal focus of attention, an external focus of attention closely related to the hand movements, and an external focus further away from the hand movements. Results showed that learning the 90° pattern involved changes in the contributions of integrated timing and error correction, whereas no changes were observed for phase entrainment. The changes in the contribution of integrated timing to the 90° pattern preceded the changes in error correction. In addition, the amount of error correction was found to increase only when integrated timing contributed to the stability and accuracy of the new pattern. These results suggested that error corrections were more effective when integrated timing provided a bimanual reference frame against which the kinesthetic feedback could be compared. Results were comparable for the three attentional focus groups. Performance of the 270° transfer pattern improved later than that of the practiced 90° pattern, suggesting that generalization to an abstract representation occurred at a slower rate than improvement of the practiced pattern itself.

Modifications of interlimb interactions were studied at an even longer time scale in Chapter 5, by examining the development of bimanual coupling from infanthood to adulthood. For this purpose, four groups were compared: 6/7-year olds, 10/11-year olds, 14/15-year olds, and young adults. Not only the temporal coupling between the hands was studied (again using tasks AB, KT, UNm, and UN), but also the spatial coupling between the hands using a bimanual line-circle drawing task. Results showed that although performance of the temporal coordination task improved over all age groups (thanks to an overall increase in coupling strength, as reflected by increased cycle duration correlation), the relative contributions of the three sources of interaction to the stability hardly changed over age. Only the absolute amount of error correction (as indexed by the error correction correlation) was found to improve with development, suggesting enhanced use of kinesthetic afference with increasing age. Furthermore, the results revealed parallel improvement of in-phase and antiphase coordination over the age groups, thereby suggesting that the differential stability of in-phase and antiphase probably evolved before the age of 6/7 years. Spatial drawing performance (as indexed by drawing smoothness and consistency) was found to improve over all age groups. Spatial coupling of the hands improved after the age of 14/15 years, as evidenced by the fact that adults showed less deterioration of bimanual drawing performance than children when bimanual drawing of spatially incompatible shapes was compared to bimanual drawing of identical shapes and to unimanual drawing. These results were consistent with the anterior-posterior direction of myelination of the corpus callosum reported in the literature, with early improvements in the temporal coupling (mediated by the anterior corpus callosum) and later improvements in the spatial coupling of the hands (more closely related to the posterior corpus callosum).

In Chapter 6 the main findings and implications of the research reported in the thesis are discussed. A major finding across the experimental studies was that the changes in the contributions of the interlimb interactions to coordinative stability were independent of the time scale over which they occurred. The differences between the contributions of the three sources of interlimb interaction seemed to depend on the intention to perform a specific bimanual pattern, because marked changes in the contributions of integrated timing and error correction, but not in phase entrainment, were evident at both short and longer time scales. Furthermore, both at a short time scale (frequency) and at a longer time scale (learning) a tight relation between integrated timing and error correction was observed. These findings were interpreted as an indication of a form of predictive control that appeared to be employed, especially during difficult coordination tasks. In this mode of control, efference copies (resulting in a bimanual frame of reference) may be used to generate sensory predictions against which actual sensory feedback can be compared. Following this discussion, Chapter 6 continues with an evaluation of the theoretical assumptions regarding interlimb interactions underlying the methodology used in the present thesis as well as its limitations. Finally in closing, several suggestions are made with regard to future directions of research, inspired by the results and insights obtained regarding the contributions of integrated timing, error correction, and phase entrainment to the stabilization of bimanual coordination.