

Error correction in bimanual coordination benefits from bilateral muscle activity: evidence from kinesthetic tracking

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Abstract Although previous studies indicated that the stability properties of interlimb coordination largely result from the integrated timing of efferent signals to both limbs, they also depend on afference-based interactions. In the present study, we examined contributions of afference-based error corrections to rhythmic bimanual coordination using a kinesthetic tracking task. Furthermore, since we found in previous research that subjects activated their muscles in the tracked (motor-driven) arm, we examined the functional significance of this activation to gain more insight into the processes underlying this phenomenon. To these aims, twelve subjects coordinated active movements of the right hand with motor-driven oscillatory movements of the left hand in two coordinative patterns: in-phase (relative phase 0°) and antiphase (relative phase 180°). They were either instructed to activate the muscles in the motor-driven arm as if moving along with the motor (active condition), or to keep these muscles as relaxed as possible (relaxed condition). We found that error corrections were more effective in in-phase than in antiphase coordination, resulting in more adequate adjustments of cycle durations to compensate for timing errors detected at the start of each cycle. In addition, error corrections were generally more pronounced in the active than in the relaxed condition. This

activity-related difference was attributed to the associated bilateral neural control signals (as estimated using electromyography), which provided an additional reference (in terms of expected sensory consequences) for afference-based error corrections. An intimate relation was revealed between the (integrated) motor commands to both limbs and the processing of afferent feedback.

Keywords Bimanual coordination · Rhythmic movement · Kinesthesia · Proprioception · Electromyography

Introduction

Recently, the relative importance of perceptual processes for motor control in general, and bimanual coordination in particular, has been intensely debated [e.g., see target article of Mechsner (2004) and associated commentaries]. Despite differences in the conceptual interpretation of empirical findings, there is ample evidence that perceptual factors affect bimanual coordination. For example, beneficial effects of augmented visual feedback on rhythmic bimanual coordination have been observed (Swinnen et al. 1997; Byblow et al. 1999; Mechsner et al. 2001), in combination with changes in concurrent neural activity (Debaere et al. 2003; Carson et al. 2005). In addition, it has been shown that perturbations of proprioception using tendon vibration result in disruption of the temporal coordination between the limbs (Verschuere et al. 1999; Steyvers et al. 2001). On the other hand, however, recent studies have indicated that important characteristics of rhythmic bimanual coordination are not primarily attributable to somatosensory feedback (Ridderikhoff et al. 2005b; Spencer et al. 2005), suggesting a key role for

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afference-independent (i.e., open-loop) control processes. Collectively, these findings motivated the present study on kinesthetic tracking, which (1) examined the closed-loop control processes underlying rhythmic bimanual coordination, and (2) addressed the potential interplay between open-loop and closed-loop control in the production of rhythmic bimanual movements.

In the present study, we focus on rhythmic bimanual movements performed at the same frequency. Such movements are characterized by the presence of only two stable coordination patterns that can be performed without training (Zanone and Kelso 1992), and that are defined in terms of the relative phase between the hands (Φ). In most cases, one pattern (in-phase coordination; $\Phi = 0^\circ$; simultaneous activation of homologous muscles) is more stable than the other pattern (antiphase coordination; $\Phi = 180^\circ$; alternated activation of homologous muscles) (Kelso 1984; Swinnen 2002). These characteristics imply that the functional consequences of various control processes can be appreciated directly in terms of their contribution to the stability difference of in-phase and antiphase coordination. In general, these control processes can be classified according to three sources of interlimb interactions. One of these sources is afference-independent, and refers to open-loop processes involved in the integrated timing of the feedforward signals to both limbs. The other two sources are associated with closed-loop processes: a reflex-like interaction resulting in phase entrainment by contralateral afference, and intentional corrections of the timing based on the perceived error in the relative phase. This conceptual framework is motivated and described in detail elsewhere (Ridderikhoff et al. 2005b). In previous studies we found that the stability difference between in-phase and antiphase coordination depended mainly on the integrated timing of the feedforward control signals (Ridderikhoff et al. 2005b), and that phase entrainment by contralateral afference did not affect this difference (Ridderikhoff et al. 2005b, 2006). As regards the second afference-based source of interlimb interactions, timing corrections based on the perceived relative phase, a more complex picture emerged, which motivated the present study as discussed in the following paragraphs.

Kinesthetic tracking tasks have been used to assess the role of afference-based interactions between the limbs in rhythmic bimanual coordination, by examining the coordination of unilateral active rhythmic movements with motor-driven oscillations of the contralateral limb (Viviani et al. 1997; Stinear and Byblow 2001; Ridderikhoff et al. 2005b). In agreement with the stability characteristics of rhythmic bimanual coordination, two previous studies on kinesthetic tracking have demonstrated differences between in-phase and antiphase coordination. One study revealed a more variable relative phase and larger response

times on a secondary task for antiphase coordination than for in-phase coordination (Stinear and Byblow 2001). The other study showed that the mean relative phase was more susceptible to an external stimulus (i.e., less stable) during antiphase coordination than during in-phase coordination (Ridderikhoff et al. 2005b). Thus, the study of kinesthetic tracking indicated that afference-based interlimb interactions may contribute to the stability difference between in-phase and antiphase coordination. In terms of the aforementioned (afference-based) sources of interlimb interaction these pattern-related stability differences should be attributed to corrections based on the perceived error in the relative phase, because phase entrainment by contralateral afference has been found to stabilize in-phase and antiphase coordination in equal measure (Ridderikhoff et al. 2005b; Ridderikhoff et al. 2006).

In our previous work we found that muscle activation patterns during kinesthetic tracking exhibited a striking similarity to the patterns observed in normal bimanual coordination, even though muscular activity was neither required nor of any consequence for the movement pattern of the motor-driven hand (Ridderikhoff et al. 2005b). In contrast, if motor-driven movements were used to induce phase entrainment by contralateral afference (i.e., when one limb was moved passively, but no coordination between the limbs was required), such activation patterns were not observed (Ridderikhoff et al. 2005b, 2006). Thus, the spontaneously adopted tendency of subjects to activate their muscles as if they were moving along with the motor-driven movement appeared directly related to the requirement of achieving a particular coordination pattern between the limbs. In principle, such spontaneous muscle activation in the driven limb may serve several purposes. It may be, for instance, that it reflects coactivation of gamma-motoneurons to enhance the sensitivity of muscle spindles (Gandevia et al. 1992). However, this possibility is less likely because several studies reported an increase of detection thresholds (Wise et al. 1998) and attenuation of muscle sense (Collins et al. 1998) during voluntary contractions (see Proske 2006 for a review). Alternatively, it may be that the activation of muscles in the motor-driven arm reflects the use of an internal control signal specifying the bimanual movement pattern. Considering that our previous work has indicated a crucial contribution of afference-independent interlimb interactions to the stability of the normal bimanual coordination (Ridderikhoff et al. 2005b), this internal control signal may well be generated reliably in an open-loop fashion. Hence, in the context of kinesthetic tracking this open-loop control signal may provide a suitable reference against which the error in the relative phasing (based on afferent signals) could be determined. Such involvement of motor commands in limb kinesthesia was recently demonstrated empirically

(Gandevia et al. 2006), and has been advocated as a fundamental principle of motor control involving predictions of the movement's sensory consequences via efference copy (e.g., Wolpert and Ghahramani 2000; Scott 2004). Note that this second account of the EMG activity in the driven limb, which in fact served as a working hypothesis for the present study, implies an intimate relation between two of the aforementioned sources of interlimb interaction, viz. error correction based on the perceived relative phase, and the integrated timing of the feedforward signals (providing the reference pattern).

The aim of the present study was to examine the efference-based error corrections in detail using a kinesthetic tracking task, with a specific focus on the role of the muscle activity in the motor-driven arm, to elucidate the interplay of closed-loop and open-loop control processes in rhythmic bimanual coordination. We compared the performance during in-phase and antiphase coordination to further our understanding of the potential contribution of closed-loop control processes to the differential stability of these patterns. In addition, we examined the stability-related effects of bilateral muscle activation during kinesthetic tracking on the resulting coordinative stability. To address the latter issue we compared two conditions in which subjects were either instructed to keep the motor-driven limb relaxed, or to activate their muscles as if moving along with the imposed motor-driven movement. For the latter condition, the phase relations at the level of neural control signals (based on electromyographic data) and at the behavioral level (kinematics) were compared. The neural control signals represent the reference signal that may be used for the prediction of sensory consequences of the ongoing movement, whereas the kinematic phase relation reflects the actual quality of the performance. In both conditions, we performed an extensive analysis of the correlations between various kinematic variables to uncover the underlying structure of the timing corrections based on the (perceived) errors in the relative phase.

Materials and methods

Subjects

Twelve healthy subjects (6 male, 6 female; aged 19–31 years) volunteered to participate. All subjects were right-handed according to their scores on a common handedness questionnaire (Oldfield 1971). They had no previous experience with the task and reported no (history of) neurological disorders. The local ethics committee approved the experiment and all subjects gave their written informed consent before the experiment was conducted.

Apparatus

Subjects sat in a height-adjustable chair with their elbows slightly flexed and their feet supported. Each forearm was placed in the apparatus in a neutral position (thumbs up and palms facing inward), and its position was restrained (by the support surface on the medial and ventral side, by two vertical foam-coated supports on the dorsal side, and by one horizontal foam-coated support on the lateral side) to prevent movements about the elbow. Both hands were fixated against the flat manipulanda using two Velcro straps, with all fingers extended. The apparatus only permitted flexion–extension movements of the wrist in the horizontal plane. The right manipulandum was mounted on a potentiometer (Sakae, type FCP40A-5k, linearity 0.1%) to register wrist joint angles during active movement, while the left was connected to a servo-controlled motor that moved the hand passively. The potentiometer's output voltage was digitized by a 12-bit ADC (Labmaster DMA) and stored on a microcomputer at a sampling frequency of 1,000 Hz. The active movements were recorded with a precision of about 0.1°. The passive movements were generated using a DC brush motor (PARVEX, type RS440GR) that was controlled by a PC-mounted servo controller (ACS-Tech80, type SB214). The maximum torque of the motor was such that subjects were unable to alter the trajectory of the applied movements, and the maximum error in the trajectory of the passive movements was 0.26°. Subjects wore earmuffs with built-in stereo earphones (Bilsom 787, Flex II), which provided a moderate level of 'white' background noise to eliminate any auditory feedback from the motion of the motor. A white opaque screen was used to eliminate visual feedback of the hand movements.

Surface electromyograms (EMG) were obtained from *M. flexor carpi radialis* (FCR), and *M. extensor carpi radialis* (ECR) of both arms. A bipolar arrangement of disposable electrodes (Medicotest, Ag/AgCl-electrodes, square 5 × 5 mm pick-up area) was attached with a center-to-center distance of 2 cm after cleansing and abrasion of the skin. The electrodes were positioned in the center of the muscle belly on the line from origin to insertion as determined by palpation. EMG signals were sampled at 1,000 Hz (TMS International, type Porti5-16/ASD; 22 bits ADC) after band-pass filtering (0.5–400 Hz), and stored on a microcomputer.

Procedure

Subjects were instructed to perform smooth oscillatory movements about the right wrist in such a way that (1) peak flexion and peak extension of both wrists were attained simultaneously (in-phase pattern), or (2) peak flexion of

one hand coincided with peak extension of the other hand (antiphase pattern). To achieve this, the timing of the active right wrist movements had to be coordinated with the motor-driven movements of the left wrist. Only subjects that were able to perform both movement patterns in at least one of two selection trials at the start of the experiment were included (one candidate subject failed to meet this criterion). After the selection trials the EMG electrodes were applied, and subsequently all subjects performed maximum voluntary contractions (MVCs) by generating an isometric flexion or extension torque with each arm for approximately 3 s. For the purpose of normalization of the EMG, the maximum root mean square (RMS) value of two separate MVC measurements was used in the analysis.

Additional instruction was given to subjects with respect to the muscle activity in the left (driven) arm. Subjects were required either to keep the muscles of the left (driven) arm as relaxed as possible (relaxed condition) or to activate the muscles of the left arm as if they were moving along with the motor-driven manipulandum (active condition). The resulting 2 (Pattern) \times 2 (Activity) = 4 conditions were performed in separate blocks of trials, the order of which was counterbalanced across subjects. Each block of trials started with at least four practice trials to familiarize the subjects with the task (if necessary, maximally four additional practice trials were allowed). Once the subject was able to perform the task properly, based on visual assessment by the experimenters, six experimental trials were performed that were used for the analysis.

For the motor-driven movements of the left wrist, sinusoidal trajectories with an average movement frequency of 1.4 Hz and mean amplitude of 35° (i.e., a range of motion of 70° about the neutral position of the wrist) were used. To create a challenging tracking task the period length and the amplitudes were varied within a trial. Because pilot experiments had shown that too much variability induced high levels of (mainly tonic) muscle activity in the relaxed condition, a moderate level of variability was selected, i.e., intermediate between natural variability and perfectly sinusoidal trajectories as used in previous studies (Ridderikhoff et al. 2005b; Stinear and Byblow 2001, respectively). Subjects started with a low level of variability in the selection trials ($SD_{\text{frequency}} = 0.02$ Hz; $SD_{\text{amplitude}} = 2^\circ$), which was increased in a step-wise fashion during the practice trials to the level of variability used in the experimental trials ($SD_{\text{frequency}} = 0.03$ Hz; $SD_{\text{amplitude}} = 5^\circ$). To assure a smooth start and finish of the trial, the amplitude of the motor-driven movements was gradually increased (from 0°) and decreased (to 0°) during the first and last 3 s of a trial, respectively. The duration of a trial was 30 s. To avoid transient effects and to exclude the cycles in which the amplitude of the passive movement was adjusted, the first 7

and the last 3 s of the trial were discarded, leaving 20 s per trial for analysis.

Data reduction (kinematics)

Figure 1 illustrates and defines the features of the time evolution of the joint angles on which the analyses of the kinematics were based. Because systematic differences in coordination were present depending on whether peak flexion or peak extension was chosen as reference, the relative phase between the hands (Φ) was calculated for each cycle as $\Phi_i = 2\pi(t_{y,i}^F - t_{x,i}^F) / (t_{x,i+1}^F - t_{x,i}^F)$ for flexion and as $\Phi_i = 2\pi(t_{y,i}^E - t_{x,i}^E) / (t_{x,i+1}^E - t_{x,i}^E)$ for extension, where $t_{y,i}$ and $t_{x,i}$ indicate the time of the i th peak flexion or peak extension of the right and left hand, respectively (for a similar method see, e.g., Carson et al. 1995). A positive relative phase meant that the right hand was lagging the left hand. Circular statistics (Mardia 1972) was used to calculate the mean and the circular standard deviation of the relative phase (SD_Φ). The absolute error of the relative phase (AE_Φ) was defined as the absolute difference between the mean relative phase and the required relative phase (0° for in-phase; 180° for antiphase).

In a previous study (Ridderikhoff et al. 2005b), we showed that kinesthetic tracking performance can also be meaningfully evaluated in terms of correlations (R_{FC} ; FC = full cycle) between the signed timing error at peak flexion or peak extension (ε_i) and the duration of the following full cycle of the right (actively moving) hand ($\Delta t_{y,i}$). The rationale behind this measure is that if an error in the relative phasing is detected at the start of the i th cycle, this error may be compensated for by adapting the duration of the next cycle, resulting in negative values of R_{FC} . Motivated by the aforementioned differences between flexion and extension that were observed for the relative phase (see also ‘‘Results’’), we also calculated the correlation between this error in the relative timing and the duration of the following half cycle of the right hand (R_{HC} ; HC = half cycle). R_{FC} and R_{HC} are intimately related in that the error correction made during a full cycle is the sum of the error corrections made during its two half cycles, provided that the latter two corrections are independent of each other. However, in general this proviso is not met, because part of the correction in the second half cycle may in fact compensate for errors that arose in the first half cycle, which is reflected by two additional temporal correlations. First, deviations in the duration of the first half cycle of the left (driven) hand (as a consequence of the variability of the imposed reference trajectory) may result in errors at the start of the second half cycle that lead to adaptation of the duration of the consecutive half-cycle of the right hand. This dependency is reflected in positive ‘‘between-hands’’

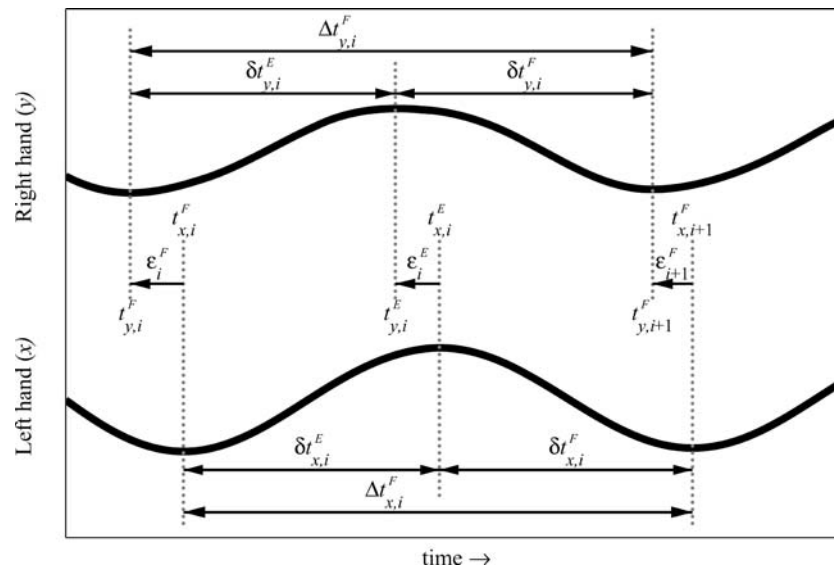


Fig. 1 Main kinematic features of one full cycle of both hands, illustrated for the in-phase coordination pattern. Moments of peak flexion and extension at the start of the i th cycle in each hand are designated by $t_{j,i}^k$, where k indicates flexion (F) or extension (E), and j refers to the right hand (y) or left hand (x). The durations of the i th full cycle between two moments of peak excursion are designated by $\Delta t_{j,i}^k$. The duration of the i th half cycle is designated by $\delta t_{j,i}^l$, where l

indicates the orientation of the hand at the end of the half cycle: flexion (F) or extension (E). The (signed) error at the start of the i th cycle is designated by ε_i^k . The definition of the (signed) errors depends on the coordination pattern and is defined in terms of the relative timing of corresponding peak excursions in both hands (flexion–flexion and extension–extension for in-phase; flexion–extension and extension–flexion for antiphase)

correlations (R_{xy}) between the durations of a half-cycle of the left (driven) hand and the following half-cycle of the right hand. Second, if in each half-cycle the errors are overcompensated, a sequence of alternating longer and shorter half-cycles is obtained. Such a dependency is reflected by negative ‘within-hand’ correlations (R_{yy}) between the successive half-cycles of the right hand. Thus, positive values of R_{xy} and negative values of R_{yy} reflect dependencies between the error corrections in successive half cycles that reduce their contributions (R_{HC}) to the full cycle error corrections R_{FC} . These four temporal correlations (R_{FC} , R_{HC} , R_{xy} , and R_{yy}) provide information about the temporal structure of the performance in terms of the timing of peak flexion and peak extension of the wrist. As such, these measures are more closely related to the underlying control processes than the global performance measures based on the relative phase. Exact definitions of (the relations between) these measures can be found in the Appendix in terms of the underlying covariances.

Because systematic differences were found between the actual timing of peak flexion and that of peak extension, the effects of these two orientations on the error correction measures (R_{FC} and R_{HC})—as obtained for timing errors at peak flexion or peak extension of the right (actively moving) hand in relation to the duration of the following (full or half) cycle of this hand—were examined as well. In addition, the effects of orientation on R_{yy} and R_{xy} were evaluated by comparing the correlations between the durations

of the two successive half-cycles following either peak flexion or peak extension of the right (actively moving) hand. In this way, the implications of R_{yy} and R_{xy} for the effects of orientation that were observed for R_{FC} could be discerned (see Appendix and Fig. 4).

Data reduction (EMG)

EMG records were bandpass filtered (10–400 Hz) using a second-order bidirectional (zero-lag) Butterworth filter (Merletti et al. 1999). To visualize the average muscle activity within a cycle, eight bins were defined in relation to the continuous phase of the movement $\Theta = \arctan[(d\theta/dt)/(2\pi f\theta)]$, where θ and $(d\theta/dt)$ are joint angle and joint angular velocity, respectively, and f is the movement frequency. Thus, each bin represented an equal part of the phase of the hand oscillation. The first bin was centered around $\Theta = 0^\circ$ (i.e., peak extension) and the fifth bin was centered around $\Theta = 180^\circ$ (i.e., peak flexion). For each bin the RMS of the EMG was calculated and normalized to that obtained for the MVC.

In addition to the comparison of conditions in terms of the average (normalized) amplitudes, the similarity of the rEMGs of homologous muscles was assessed using the weighted coherence. Specifically, the weighted coherence reflects the degree of similarity (or phase locking) of the activity bursts in the homologous muscles in terms of a weighted average of the coherence in the vicinity of the

movement frequency (i.e., in the frequency band in which these bursts occur), yielding values between 0 (no phase locking) and 1 (perfect phase locking). Thus, the weighted coherence is an estimate of the strength of the interlimb coupling at the level of the neural control signals (Ridderikhoff et al. 2005b). In the present study it was used to evaluate differences in this regard between the relaxed and active conditions and between flexor and extensor muscles. The weighted coherence (Porges et al. 1980) of the full-wave rectified EMG (rEMG) of homologous muscles (C_W) was calculated as

$$C_W = \frac{\int_{f-\Delta f}^{f+\Delta f} C_{xy}(f')P_y(f')df'}{\int_{f-\Delta f}^{f+\Delta f} P_y(f')df'}$$

where Δf defines a bandwidth around the movement frequency f ($\Delta f = 0.1$ Hz). P_y is the power spectrum of the rEMG of the right arm, and C_{xy} is the coherence of the rEMGs of the homologous muscles in the left and right arm. The power spectra and the coherence were estimated with Welch's modified periodogram method (Oppenheim and Schaffer 1975) using a Hanning window of three cycles.

In addition, the phase relations between rEMGs and joint angles θ were studied to compare the temporal relations observed at the level of the neural control signals to those observed at the behavioral level. This is of particular importance for the analysis of the contribution of the bilateral motor commands to the performance in the active condition. The phase shift between rEMG and θ was obtained from the cross-spectrum of rEMG and θ estimated at the movement frequency (using the same parameters as for the weighted coherence). Because flexion corresponded to negative values of θ , the phase shift between the EMG of FCR and θ was adjusted by 180° (cf. Ridderikhoff et al. 2004). Likewise, the relative phases between the rEMGs of homologous muscles were determined from the cross-spectrum of rEMGs of muscles in the left and right arm. The constant error of these relative phases was defined as the signed difference between the mean relative phase and the required relative phase (0° for in-phase; 180° for anti-phase), with negative values indicating a relative phase lead of the activity in the right arm. The calculation of these measures required that the signals in question were phase and frequency locked, which implied that both measures could only be obtained for the active condition because only in this condition the rEMG of the muscles in the left (motor-driven) arm satisfied this requirement. For both measures (i.e., the phase shifts between rEMG and θ , and the relative phases between rEMGs of homologous muscles) the values obtained for FCR and ECR were

analyzed separately to examine differences in the relative timing of flexors and extensors in relation to effects of coordinative pattern (for both measures) and limb (for the phase shifts between rEMG and θ). In addition, the values obtained for FCR and ECR were averaged to obtain a global measure for the phasing of the neural control signals to the limbs (Viviani et al. 1976). To visualize the main temporal relations in the movement system, the relative phase between the neural control signals, the phase shifts between the neural control signals and the movements of the left and right hand, and the average relative phase between the hands were examined in conjunction.

In the active condition, FCR of the left (driven) arm of two subjects showed substantial reactive activity comparable in magnitude to that observed in the relaxed condition (see Fig. 5c; peak at bin 5, open symbols) in addition to the normal timing of muscle activation that was required in this condition (see Fig. 5c; peak at bin 2, filled symbols). This reactive activity was to some extent present in most subjects (as indicated by the peaks in Fig. 5, which was created without using the data of these two excluded subjects), but typically much less pronounced. For the two excluded subjects the large amplitude of the reactive activity resulted in a shift of the dominant frequency of the power spectrum of left FCR in this condition to twice the movement frequency (i.e., two bursts per cycle). The EMG data of these subjects were excluded from the analyses, because their inclusion resulted in a number of additional significant effects that could all be attributed to this reactive activity, but were not representative for the EMG data of the group as a whole. It should be noted, however, that all phenomena mentioned in the Results section were also observed for the excluded subjects.

Statistical analysis

Statistical analyses of the kinematics were performed using a 2 (Pattern: in-phase vs. antiphase coordination) \times 2 (Activity: active vs. relaxed) \times 2 (Orientation: flexion vs. extension) repeated measures analysis of variance (ANOVA). Also EMG-related measures were analyzed with repeated measures ANOVAs involving various, question-specific designs, which are described in the corresponding subsections of the Results. To facilitate the interpretation of the results obtained with ANOVA, paired-sample t -tests were used for post hoc analysis of the significant results ($P < 0.05$), and effect sizes (f) were calculated in terms of the partial η^2 (Cohen 1988). The correlations were transformed to normally distributed variables using the Fisher transform. The same transformation was applied to the weighted coherence (Rosenberg et al. 1989). Whereas the inferential analyses were based on the transformed values, the corresponding untransformed values (bounded on the

interval $[-1, 1]$ for the correlations and on the interval $[0, 1]$ for the coherence) are presented for reasons of clarity.

Results

Adequate performance of a trial was determined using the following inclusion criteria: (1) the number of cycles performed by the right hand and the (driven) left hand should be the same (i.e., no phase wrapping); (2) AE_{Φ} should be smaller than 60° , and (3) the within-trial fluctuations of the relative phase should be within a range of 90° . In total 25 trials (8.7%) were excluded from the analysis: 9 trials in the active condition (3 trials for in-phase coordination, and 6 trials for antiphase coordination); 16 trials in the relaxed condition (7 trials for in-phase coordination, and 9 trials for antiphase coordination). In each condition all subjects were capable of performing the task in at least three trials in an adequate fashion.

Relative phase

Statistical analysis of AE_{Φ} (see Fig. 2a) revealed a significant effect of Activity ($F(1, 11) = 5.38$; $P < 0.05$; $f = 0.70$), indicating that AE_{Φ} was larger for the active condition (mean \pm between-subjects SD: $28.2^{\circ} \pm 11.1^{\circ}$) than for the relaxed condition ($20.6^{\circ} \pm 12.5^{\circ}$). In addition,

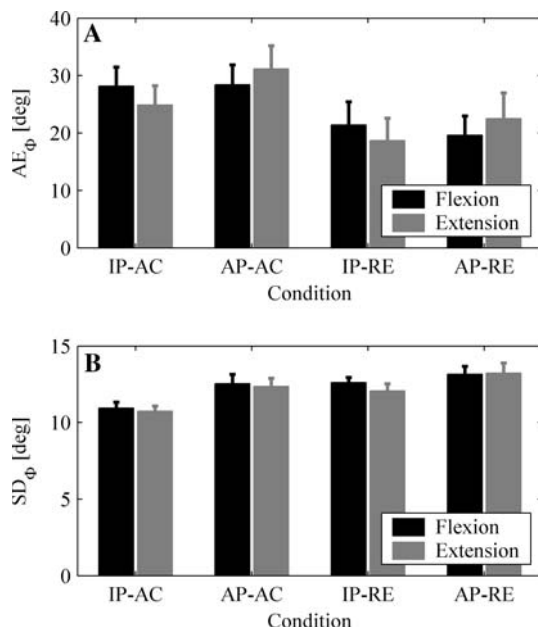


Fig. 2 **a** Mean absolute error of the relative phase (AE_{Φ}). **b** Standard deviation of the relative phase (SD_{Φ}). Results obtained for the relative timing of peak flexion (black bars) and peak extension (gray bars) are shown for in-phase (IP) and antiphase (AP), both for the conditions in which the muscles of the left hand were active (AC) or relaxed (RE). Error bars indicate the standard error of the mean

a significant Pattern \times Orientation interaction was found ($F(1, 11) = 6.44$; $P < 0.05$; $f = 0.77$). Post hoc analysis demonstrated two significant differences underlying this interaction, viz. between in-phase and antiphase coordination at peak extension ($21.8^{\circ} \pm 11.0^{\circ}$ vs. $26.8^{\circ} \pm 11.1^{\circ}$, respectively) and between flexion and extension during antiphase coordination ($24.0^{\circ} \pm 10.0$ vs. $26.8^{\circ} \pm 11.1^{\circ}$, respectively). The same statistical results were obtained for the constant errors in relative phasing (not shown), because the errors were almost always in the same direction (i.e., negative), indicating that the right (actively moving) hand was leading in time.

To examine the stability of the coordinative patterns statistical analysis of SD_{Φ} (see Fig. 2b) was conducted, which revealed significant effects of Activity ($F(1, 11) = 5.94$; $P < 0.05$; $f = 0.74$) and Pattern ($F(1, 11) = 14.61$; $P < 0.005$; $f = 1.15$). These effects resulted from, respectively, a larger SD_{Φ} in the relaxed condition than in the active condition ($12.7^{\circ} \pm 1.4^{\circ}$ vs. $11.7^{\circ} \pm 1.4^{\circ}$) and a larger SD_{Φ} for antiphase coordination than for in-phase coordination ($12.8^{\circ} \pm 1.5^{\circ}$ vs. $11.6^{\circ} \pm 0.87^{\circ}$).

Movement amplitude

To examine whether the different activity levels of the muscles in the left (driven) arm had an effect on the amplitude of the movements about the right wrist, the range of motion (i.e., the difference in peak extension and peak flexion) was determined for each cycle, averaged per condition and subjected to a 2 (Pattern) \times 2 (Activity) repeated measures ANOVA. The analysis solely revealed a significant effect of Activity ($F(1, 11) = 37.00$; $P < 0.001$; $f = 1.83$), resulting from a larger movement amplitude in the active condition than in the relaxed condition (range of motion: $85.5^{\circ} \pm 23.8^{\circ}$ vs. $58.6^{\circ} \pm 14.4^{\circ}$, respectively).

Temporal correlations between kinematic variables

The average correlations between the signed error and the duration of the following full cycle (R_{FC}) or half cycle (R_{HC}) are shown in Fig. 3a, b, respectively. Statistical analysis of R_{FC} revealed significant effects for Activity ($F(1, 11) = 7.05$; $P < 0.05$; $f = 0.80$), Pattern ($F(1, 11) = 5.29$; $P < 0.05$; $f = 0.69$) and Orientation ($F(1, 11) = 13.35$; $P < 0.01$; $f = 1.10$). R_{FC} was more pronounced (larger absolute values) for the active condition than for the relaxed condition (-0.76 ± 0.14 vs. -0.69 ± 0.14), for the in-phase pattern than for the antiphase pattern (-0.76 ± 0.14 vs. -0.69 ± 0.13), and for errors at peak flexion than for errors at peak extension (-0.75 ± 0.14 vs. -0.70 ± 0.14).

Statistical analysis of R_{HC} revealed significant effects for Activity ($F(1, 11) = 13.33$; $P < 0.01$; $f = 1.10$) and Pattern ($F(1, 11) = 13.02$; $P < 0.01$; $f = 1.09$), indicating

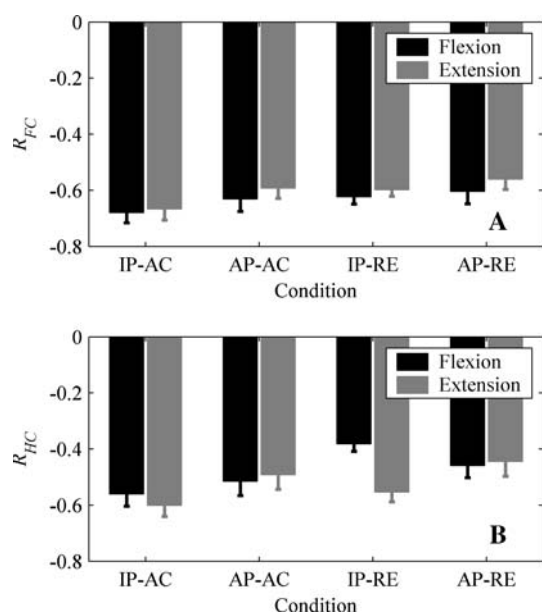


Fig. 3 Mean correlations between the signed timing error and the duration of the following full cycle (R_{FC} , **a**) or half cycle (R_{HC} , **b**) of the right (actively moving) hand. Results are shown for in-phase (IP) and antiphase (AP), both for the conditions in which the muscles of the left hand were active (AC) or relaxed (RE). R_{FC} was calculated for full cycles following the error at two different orientations of the right (actively moving) hand: peak flexion (black bars) and peak extension (gray bars). R_{HC} was calculated for the flexion half cycles following the error at peak extension (black bars) and the extension half cycles following the error at peak flexion (gray bars). Error bars indicate the standard error of the mean

larger absolute values for the active condition than for the relaxed condition (-0.61 ± 0.17 vs. -0.50 ± 0.17), and for the in-phase pattern than for the antiphase pattern (-0.59 ± 0.17 vs. -0.52 ± 0.17). In addition, for R_{HC} significant Activity \times Pattern ($F(1, 11) = 6.14$; $P < 0.05$; $f = 0.75$) and Pattern \times Orientation ($F(1, 11) = 9.12$; $P < 0.05$; $f = 0.91$) interactions were found. Post hoc analysis revealed that the first interaction effect resulted from a larger absolute value of R_{HC} for in-phase coordination in the active condition than for the three other combinations of Activity and Pattern (see Fig. 3b). The second interaction effect was due to a larger absolute value of R_{HC} for the extension half-cycle in the in-phase pattern than for the three other combinations of Pattern and Orientation (see Fig. 3b).

The main effects of Activity and Pattern were qualitatively the same for R_{HC} and R_{FC} , but the effect of Orientation was markedly different. An explanation of this difference was found in a formal analysis of the relation between the covariances¹ underlying R_{HC} and R_{FC} , which

¹ Additional analyses indicated that the observed differences indeed resulted from the covariances on which these correlations were based, and not from differences in the normalization factors (i.e., the standard deviations of the variables involved).

demonstrated that (unlike differences related to Activity or Pattern) differences between flexion and extension in R_{HC} are completely unrelated to those in R_{FC} (see Appendix). Two additional factors are involved in the relation between R_{HC} and R_{FC} (see “Materials and methods” and Appendix), which were captured by the within-hand and between-hands correlations of the durations of successive half cycles (R_{yy} and R_{xy} , respectively). The effect of Orientation in R_{FC} can be attributed completely to (the covariances underlying) R_{yy} and R_{xy} (see Appendix). However, also for the other factors (Activity and Pattern) the relation between R_{HC} and R_{FC} may be affected by R_{yy} and R_{xy} , given the potential dependencies between error corrections in successive half-cycles. Thus, the temporal correlations were examined further in terms of the within-hand correlation R_{yy} and the between-hands correlation R_{xy} .

Analysis of the between-hands correlation R_{xy} (Fig. 4b) revealed no significant effects. In contrast, significant effects of Activity ($F(1, 11) = 8.83$; $P < 0.05$; $f = 0.90$) and Orientation ($F(1, 11) = 8.19$; $P < 0.05$; $f = 0.86$) were found for the within-hand correlation R_{yy} . The effect of Activity revealed that the values of R_{yy} for the active condition were more negative than for the relaxed condition (-0.16 ± 0.17 vs. -0.02 ± 0.07). The effect of Orientation indicated that the correlations between the extension half cycle and the following flexion half cycle were more negative (-0.14 ± 0.10 ; gray bars in Fig. 4a) than those between the flexion half cycle and the following extension half cycle (-0.02 ± 0.17 ; black bars in Fig. 4a). The consequences of R_{yy} and R_{xy} for R_{FC} are illustrated in Fig. 4c, d, respectively, which show the contributions of the covariances underlying R_{yy} and R_{xy} to R_{FC} , according to the relations derived in the Appendix. The temporal relations expressed by R_{yy} and R_{xy} both result in a reduction of R_{FC} (i.e., they reduce the effects of the half cycle error corrections, see “Materials and methods”); the effect of the former being larger than that of the latter (compare Fig. 4c, d). Both correlations resulted in a larger reduction of R_{FC} for errors at peak extension than for errors at peak flexion, which explains the aforementioned effect of Orientation obtained for R_{FC} . In addition, the effect of Activity for R_{yy} revealed that the error corrections in successive half-cycles were more correlated for the active condition than for the relaxed condition. This implied that in particular in the active condition a part of the adjustments of the half-cycle durations (captured by R_{HC}) compensated for overcorrection in the preceding half-cycle.

EMG

The average amplitudes of the EMGs (normalized to MVC amplitude) during the movement cycle are presented in Fig. 5, which exposes five noteworthy characteristics of the

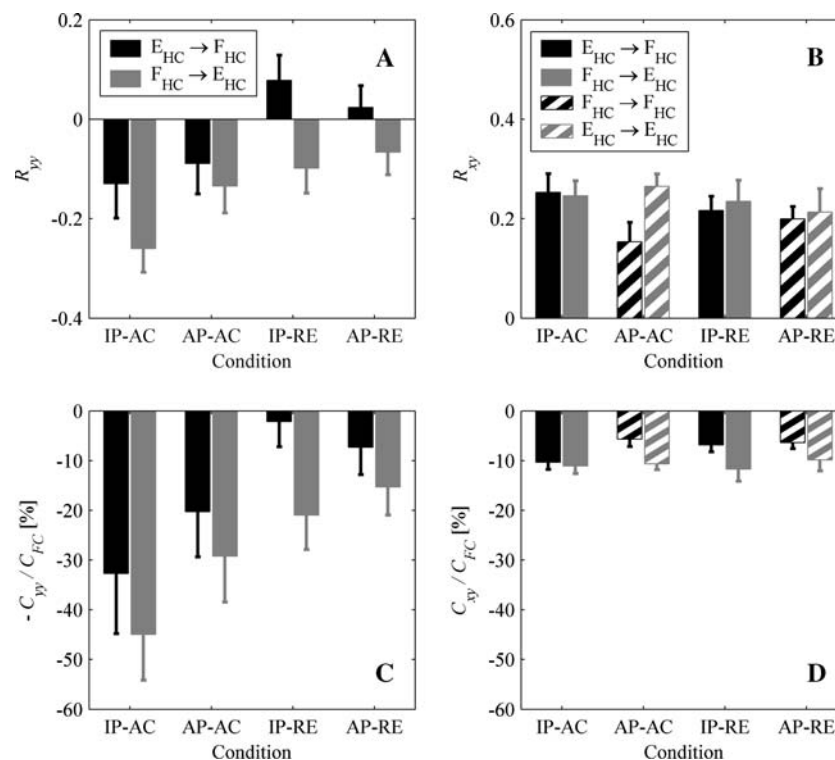


Fig. 4 Mean correlations of the durations of successive half-cycles obtained during in-phase (IP) and antiphase (AP) coordination, while the muscles of the left (driven) hand were active (AC) or relaxed (RE): **a** within-hand correlations (R_{yy}); **b** between-hands correlations (R_{xy}). **c** and **d** indicate the relative contributions of the covariances underlying the within-hand and between-hands factors (C_{yy} and C_{xy} , respectively) by expressing them as a fraction of the covariance underlying R_{FC} (i.e., C_{FC}): negative values indicate a reduction of the absolute value of R_{FC} (see Appendix). To facilitate comparison the

values of R_{yy} and R_{xy} are presented in the same order as the corresponding values of R_{FC} in Fig. 3. Error bars indicate the standard error of the mean. The legends of **a** and **b** also apply to **c** and **d**, respectively. Legends: F_{HC} = flexion half cycle; E_{HC} = extension half cycle; the arrows specify the temporal order of the half cycles. Whereas the second half cycle is always performed by the right hand, the first half cycle is performed either by the right hand (R_{yy} and C_{yy} , **a** and **c**) or by the left hand (R_{xy} and C_{xy} , **b** and **d**)

EMG data. First, in the right arm the EMG amplitudes were smaller in the relaxed condition than in the active condition (compare open and filled symbols, respectively, in Fig. 5a, b), corresponding to the observed differences in range of motion between these conditions. Second, in line with the task requirements, the EMG amplitudes of the muscles in the left arm were in general much smaller in the relaxed condition than in the active condition (compare open and filled symbols, respectively, in Fig. 5c, d). Third, for left FCR in the relaxed condition a distinctive (reactive) peak in the EMG amplitude was observed at bin 5, i.e., the moment at which the lengthening of the muscle started (open symbols in Fig. 5c). Fourth, for left ECR in the relaxed condition the EMG amplitude showed a slight modulation during the movement cycle that mimicked that of normal activation patterns (compare open symbols in Fig. 5d with the curves in Fig. 5b). Fifth, both left FCR and ECR in the active condition (filled symbols in Fig. 5c, d, respectively) were shifted leftward with respect to the (motor-driven) movement compared to the timing of right FCR and ECR when compared to the (self-generated)

movement (Fig. 5a, b, respectively). Note that this phase advance of the EMG in the left arm relative to the corresponding hand motion was possible because (in contrast to the right hand) the movements of the (motor-driven) left hand were completely independent of its muscle activity.

Weighted coherence

The weighted coherence of the rEMG of homologous muscles is shown in Fig. 6. Statistical analysis using a 2 (Pattern) \times 2 (Activity) \times 2 (Muscle) repeated measures ANOVA revealed significant effects of Activity ($F(1, 9) = 103.98$; $P < 0.001$; $f = 3.39$) and Muscle ($F(1, 9) = 17.70$; $P < 0.01$; $f = 1.40$), as well as a significant Activity \times Pattern interaction ($F(1, 9) = 10.68$; $P < 0.05$; $f = 1.09$). The effect of Activity revealed that the weighted coherence was larger in the active condition than in the relaxed condition (0.85 ± 0.25 vs. 0.54 ± 0.63). The effect of Muscle showed that the weighted coherence was larger for ECR than for FCR (0.77 ± 0.38 vs. 0.62 ± 0.54), indicating a greater similarity of the EMG activity for

Fig. 5 Normalized EMG amplitudes (RMS values) of FCR (**a** right; **c** left) and ECR (**b** right; **d** left), averaged over subjects, at eight phases of the movement cycle. Each graph shows the muscle activity for the conditions in which the muscles of the left (driven) arm were either active (*filled symbols*) or relaxed (*open symbols*), for in-phase (*triangles; solid lines*) and antiphase coordination (*circles; dashed lines*) separately

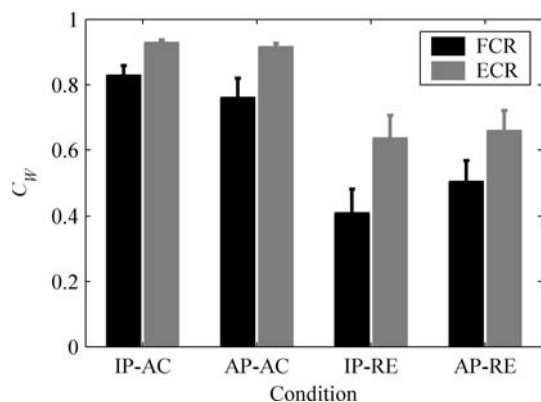
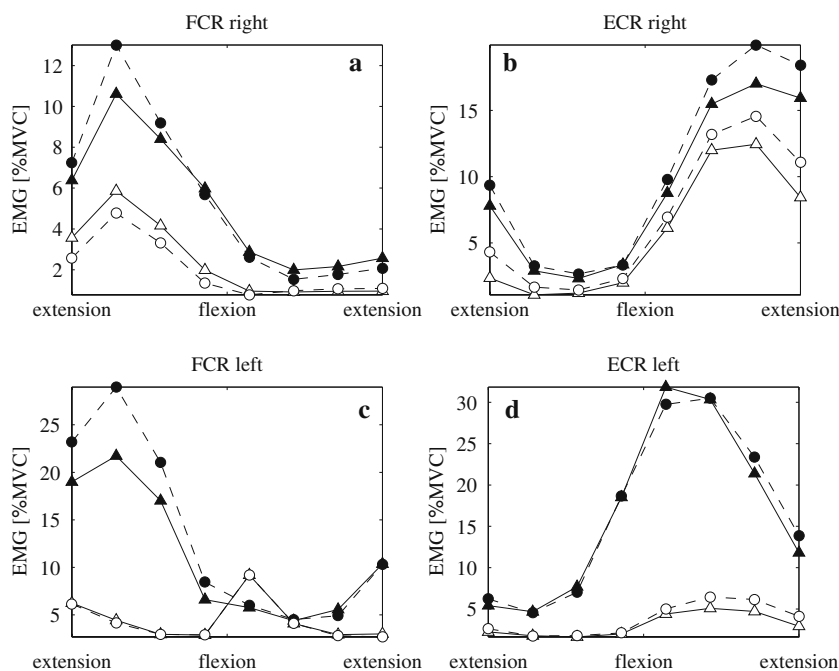


Fig. 6 Mean weighted coherence (C_w) of the rectified EMGs of homologous muscles: FCR (*black*) and ECR (*gray*) during in-phase (IP) and antiphase (AP) coordination, both for the conditions in which the muscles of the left (motor-driven) hand were active (AC) or relaxed (RE). Error bars indicate the standard error of the mean

extensor than for flexor muscles. Post hoc analysis of the Activity \times Pattern interaction revealed no significant differences between in-phase and antiphase coordination for either the active condition or the relaxed condition (or vice versa), although the weighted coherence was larger for in-phase than for antiphase in the active condition (0.86 ± 0.22 vs. 0.83 ± 0.32), but smaller for in-phase than for antiphase in the relaxed condition (0.51 ± 0.22 vs. 0.57 ± 0.60).

Temporal relations in the active condition

In the active condition, the relative phase was determined at two levels: at the behavioral level (kinematics) and at the

level of the neural control signals (based on rEMG). This distinction is important because for the right hand the phase shift between EMG activity and kinematics was constrained by the effector dynamics of the wrist (Ridderikhoff et al. 2004), whereas these constraints did not affect the phase shift for the left (motor-driven) hand. Hence, the two levels were not tightly coupled in this kinesthetic tracking task. To examine the relations between these levels, four different phase relations were studied in conjunction: the phase shifts between neural control signals and behavior for (1) the right hand and (2) the left hand, and the relative phase between the limbs at (3) the behavioral level and (4) the level of neural control signals. The results regarding the relative phase at the behavioral level were presented in the preceding. In the next two subsections the other phase relations (i.e., the phase shifts between rEMG and kinematics and the relative phase between rEMGs of homologous muscles) are presented. The results are combined in the final subsection to provide an overall picture of the temporal relations in the active condition across these different levels.

Phase shifts between EMG and kinematics

In the active condition differences between the left and right hand were observed with respect to the timing of the muscle activity relative to the ongoing movement (see Fig. 5). To analyze these differences, the phase shifts between rEMG and kinematics (see Table 1; negative values indicate that the EMG is leading the kinematics) were examined using a 2 (Hand) \times 2 (Pattern) \times 2 (Muscle)

Table 1 Phase shifts between rectified EMG and joint angles in the active condition (mean \pm between-subjects SD) as determined from the cross-spectrum of these variables at the movement frequency

Hand	Muscle	In-phase	Antiphase
Left	FCR	$-148.2^\circ \pm 22.1^\circ$	$-137.5^\circ \pm 22.5^\circ$
	ECR	$-151.7^\circ \pm 27.8^\circ$	$-143.7^\circ \pm 33.5^\circ$
Right	FCR	$-123.1^\circ \pm 14.2^\circ$	$-131.6^\circ \pm 17.7^\circ$
	ECR	$-103.5^\circ \pm 17.7^\circ$	$-99.5^\circ \pm 15.2^\circ$

repeated measures ANOVA. This revealed a significant effect of Hand ($F(1, 9) = 11.79$; $P < 0.01$; $f = 1.14$), indicating larger phase shifts for the left hand than for the right hand (-145.3° vs. -114.4°). In addition, significant Hand \times Muscle ($F(1, 9) = 14.21$; $P < 0.01$; $f = 1.26$), Hand \times Pattern ($F(1, 9) = 6.24$; $P < 0.05$; $f = 0.83$), and Hand \times Pattern \times Muscle ($F(1, 9) = 6.08$; $P < 0.05$; $f = 0.82$) interactions were found. Post hoc analysis demonstrated that the Hand \times Muscle interaction occurred because the phase shifts for ECR and FCR differed significantly for the right hand ($-101.5^\circ \pm 21.2^\circ$ vs. $-127.4^\circ \pm 14.9^\circ$), but not for the left (motor-driven) hand. The Hand \times Pattern interaction post hoc analysis revealed that the phase shifts during in-phase and antiphase coordination differed significantly for the left (motor-driven) hand ($-149.9^\circ \pm 23.7^\circ$ vs. $-140.6^\circ \pm 27.2^\circ$), but not for the right hand. Post hoc analysis of the three-way interaction revealed that the phase shift for the left FCR during antiphase coordination deviated from the overall pattern: it was significantly different from the phase shift during in-phase coordination (in the absence of significant differences between in-phase and antiphase for any of the other muscles), and it was not significantly different from the phase shift for right FCR during antiphase coordination (whereas all other left-right comparisons yielded significant differences for both coordinative patterns).

Relative phasing of EMG

The relative phase between the rEMG of homologous muscles in the active condition was calculated for FCR and ECR. The constant errors with respect to the reference values for in-phase (0°) and antiphase (180°) coordination (see Table 2) were subjected to a 2 (Pattern) \times 2 (Muscle) repeated measures ANOVA. The analysis revealed significant effects of Pattern ($F(1, 9) = 12.19$; $P < 0.01$; $f = 1.16$), Muscle ($F(1, 9) = 16.20$; $P < 0.01$; $f = 1.32$), and a significant Pattern \times Muscle interaction ($F(1, 9) = 5.23$; $P < 0.05$; $f = 0.76$). The effect of Pattern resulted in a significantly larger constant error for in-phase than for antiphase coordination ($12.5^\circ \pm 18.0^\circ$ vs. $0.3^\circ \pm 24.0^\circ$; positive values indicate a relative phase lead of the activity

Table 2 Mean constant errors in the relative phase for kinematics and EMG in the active condition (mean \pm between-subjects SD)

Level	In-phase	Antiphase
Kinematics	$-22.7^\circ \pm 10.4^\circ$	$-24.8^\circ \pm 11.4^\circ$
EMG		
FCR	$0.1^\circ \pm 26.2^\circ$	$-18.8^\circ \pm 28.5^\circ$
ECR	$24.9^\circ \pm 19.0^\circ$	$19.4^\circ \pm 24.7^\circ$
Mean	$12.5^\circ \pm 18.0^\circ$	$0.3^\circ \pm 24.0^\circ$

For the EMG the obtained values are presented for homologous FCR and ECR separately. The mean of the constant errors for FCR and ECR was adopted as the constant error of the neural control signal. Negative (positive) values indicate that the right limb is leading (lagging) the left limb

in the left arm). The effect of Muscle indicated that the average constant errors for FCR and ECR were significantly different ($-9.3^\circ \pm 26.9^\circ$ vs. $22.2^\circ \pm 20.6^\circ$). Post hoc analyses of the Pattern \times Muscle interaction revealed a significant difference between the constant errors for in-phase and antiphase coordination for FCR but not for ECR (see values in Table 2).

Relative phasing of neural control signals and behavior

To gain insight into the neurobehavioral basis of error correction, we examined the phase relations between the neural control signals and the overt behavior in the active condition. For this purpose, the phasing of the neural control signals was estimated for each limb separately by taking the average of the values obtained for FCR and ECR (see Tables 1, 2). The resulting phase relations are displayed schematically for in-phase and antiphase coordination in Fig. 7, which illustrates the muscle-independent phase relations addressed in the previous two paragraphs, showing only the effects of Hand and Pattern. First, the phase shift between the neural control signal and the wrist movements was larger for the (motor-driven) left hand (dashed arrows) than for the right hand (solid arrows)—significant effect of Hand. Second, the constant error in relative phase between the EMGs of homologous muscles was larger for in-phase than antiphase coordination (compare the corresponding diagrams)—significant effect of Pattern. Third, it can be appreciated from the figure that the phase shift between EMG and kinematics (larger shifts in the left hand, i.e., longer dashed arrows, for in-phase than for antiphase coordination) depended on the combination of hand and pattern—significant Hand \times Pattern interaction. Finally, the diagrams indicate that, on average, the error in the relative phase was smaller for the neural control signal than for the kinematics (respective values are presented in Table 2).

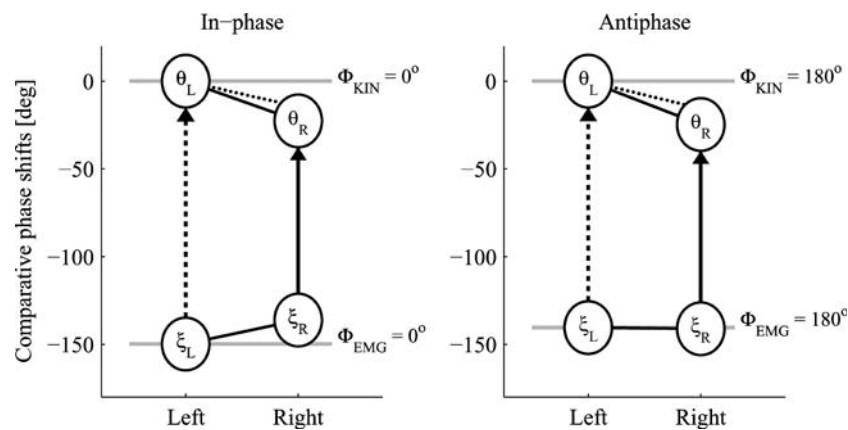


Fig. 7 Diagrams illustrating temporal relations in the active condition for in-phase (*left panel*) and antiphase (*right panel*) coordination. Circles represent signal sources: θ is the joint angle, and ξ is the neural control signal (derived from the EMG, averaged over FCR and ECR). The length of the arrows indicates the phase shifts between the neural control signal and the kinematics (arrows point in the direction

of time). The error of the relative phase Φ is equal to the inclination angle of the line connecting the circles at either the kinematic (θ) or the control level (ξ). The target values of Φ are indicated by the gray horizontal lines, and the dotted lines represent the relative error in Φ in the relaxed condition (available for kinematics only)

Discussion

The goal of the present study was to gain more insight into the error correction processes as allegedly implicated in bimanual coordination (Ridderikhoff et al. 2005b). To this end, we examined the temporal adjustments of the actively moving (right) limb in a kinesthetic tracking task based on the perceived (error in the) relative phase between the limbs. In particular, subjects tracked their motor-driven left hand with the actively moving right hand to achieve in-phase or antiphase coordination, in conditions where the left hand musculature was activated (as if moving along with the reference movement) or kept as relaxed as possible. In addition, the relation between bimanual (between-limbs) and unimanual (within-limb) factors was examined. Unimanual and bimanual factors were dissociated by comparison of several (related) temporal correlations and by examining the phase shifts between neural control signals and kinematics both within and between limbs. In line with our research questions the analysis focused on two aspects of the measurements, which are discussed in detail in the next two subsections: (1) differences in error correction between in-phase and antiphase coordination, and (2) effects of muscle activity in the driven (left) limb on these error corrections and on the overall performance of the task. In the last two subsections, we will then address the observed differences between the left and right hand and between flexors and extensors in terms of the phase shifts between EMG and kinematics and the relative timing of flexion and extension. Before embarking on these discussions, it should be noted that the stability of the bimanual patterns was affected by the muscle activity in the motor-driven limb, as SD_Φ was larger in the relaxed condition than

in the active condition. Furthermore, the variability of the relative phase (SD_Φ) was smaller for in-phase than for antiphase coordination. This basic observation confirmed the result of an earlier study on kinesthetic tracking (Stinear and Byblow 2001) and indicated that also in normal bimanual coordination the stability difference of in-phase and antiphase coordination may be partly dependent on afference-based error corrections.

Error corrections

We performed an in-depth analysis of the corrections in the timing of the movements of the right (actively moving) limb based on the perceived errors in the relative phase. Since our analyses of the kinematics concerned the timing of discrete events (i.e., peak extension and peak flexion), the shortest possible time scale to study error corrections was related to compensatory adjustments of the duration of the half-cycle following the detected error. The related measure (R_{HC}) indicated that the error corrections were more pronounced for in-phase than for antiphase coordination and that they were characterized by larger absolute values for the active condition than for the relaxed condition, in line with the observed effects for SD_Φ . Additional analysis of the compensatory adjustments of the duration of the full cycle following the detected error (R_{FC}) showed that both error correction effects persisted on a longer time scale. Therefore, we conclude that corrections in the movement timing of the right hand based on the perceived errors in the relative phase underlie the observed stability effects (SD_Φ) of the examined coordination patterns (in-phase vs. antiphase) and muscle activity.

It is important to consider error corrections at different time scales, because the dependency of the corrections performed in successive half-cycles may vary over conditions (see “[Materials and methods](#)”). The results revealed that in the present study these dependencies between successive half-cycles were reflected mainly by the within-hand correlation R_{yy} , indicating an important role for the unimanual coordinative processes underlying the rhythmic movements of the right hand. This role is of particular importance for the interpretation of the significant Pattern \times Activity interaction observed for R_{HC} , suggesting more pronounced error corrections during in-phase coordination in the active condition. Because the results obtained for R_{yy} demonstrated larger dependencies between successive half-cycles in the active condition than in the relaxed condition, the effects related to muscle activity were reduced at a longer time scale (R_{FC}). As a consequence, the Pattern \times Activity interaction was not significant for R_{FC} and, thus, appeared to be of little functional relevance in terms of the coordinative stability. This illustrates how unimanual coordination (the flexion–extension coupling in terms of R_{yy}) may impinge on the effects of interlimb interactions (the error corrections in terms of R_{HC}) in bimanual coordination.

Two additional discrepancies between R_{HC} and R_{FC} were found in relation to effects of the orientation of the hand (flexion or extension). This was not surprising, because R_{HC} and R_{FC} are unrelated by definition with respect to these effects. As shown both analytically (for the underlying covariances, see Appendix) and empirically all differences between flexion and extension in R_{FC} are attributable to the correlations between the durations of successive half-cycles within the right hand (R_{yy}) and between hands (R_{xy}). Specifically, the effect of orientation of the hand obtained for R_{FC} was not related to error corrections based on the perceived relative phase, but rather reflected an asymmetry in the coupling of the unimanual flexion and extension half-cycles as captured by R_{yy} . In contrast, differences in the strength of the error corrections during the flexion and extension half-cycles are indicated by effects of orientation observed for R_{HC} . Analysis of R_{HC} revealed a significant Pattern \times Orientation interaction, which indicated more pronounced error corrections in the half-cycle following peak flexion of the left (motor-driven) hand, in particular in the extension half-cycle during in-phase coordination (Fig 3b). In line with this result, we observed the smallest errors in the mean relative phase at the end of the half-cycles with the most prominent error corrections (i.e., at peak extension during in-phase and at peak flexion during antiphase coordination; see Fig 2a). A tentative explanation of these findings is that (relative) timing errors were detected most accurately at peak flexion of the driven hand and that, as a consequence, the correc-

tions in the following half-cycle were most effective, leading to the highest accuracy in the relative phase at the end of these half-cycles.

With respect to the two adopted measures of error correction (R_{HC} and R_{FC}) these analyses demonstrated that both measures should be evaluated in conjunction to assess the net effect of error corrections in relation to the effects of movement pattern and muscle activity, whereas R_{HC} offers additional insight into the differences between flexion and extension in this respect. The analyses of the temporal correlations revealed several important global characteristics of the afference-based error corrections underlying rhythmic bimanual coordination. Although the analyses demonstrated that error corrections occur during the next half-cycle, it is important to emphasize that the precise time course of the error corrections remains unknown. That is, these methods do not reveal how long it takes until the ongoing movements are adapted to compensate for perceived errors, except for showing that such changes occur within the next half-cycle. Although, in principle, it is possible that timing errors are detected throughout the cycle and not only at peak flexion and peak extension, there is ample evidence indicating that coordinated rhythmic movements are characterized by the presence of so-called anchor points (Beek 1989), that is, discrete points in the cycle that have particular significance for the control of timing. Furthermore, several studies have demonstrated that anchoring occurs when peak flexion and/or peak extension are coinciding with an external stimulus (Byblow et al. 1994; Fink et al. 2000). These findings provide a rationale for the use of the moments of peak flexion and peak extension in the analysis of the temporal structure of the bimanual coordination pattern, and the instructions to subjects in terms of the timing of peak flexion and peak extension (see “[Materials and methods](#)”) may have helped to establish such anchor points in the present study. However, further research regarding the existence of anchor points in the processing of kinesthetic feedback and the time course of the adjustments is required, for which the analyses in the present study may serve as departure point. For our current purposes, R_{HC} and R_{FC} provided important insights into the average amount of corrective activity that occurs at two relevant time scales in terms of the same kinematic measures that were used to assess the performance in terms of the relative phase between the hands.

The effects of muscle activity in the driven limb

The second objective of this study was to examine the neurobehavioral basis of error correction. To this aim, we manipulated the muscle activity in the motor-driven limb by instructing subjects either to activate their muscles in accordance with the ongoing motion or to keep them as

relaxed as possible. The average EMG amplitudes (Fig. 5) clearly showed that this manipulation of muscle activity was successful in the sense that subjects managed by and large to avoid activating the muscles in the motor-driven left hand in the relaxed condition. This was further underscored by the fact that the values of the weighted coherence of rEMGs of homologous muscles in the relaxed condition did not exceed those obtained in previous studies involving passive (i.e., motor-driven) hand movement (Ridderikhoff et al. 2005b; Ridderikhoff et al. 2006). In those studies subjects had been explicitly instructed to ignore the motor-driven movement (i.e., no coordination between the hands was required) in order to study phase entrainment by contralateral afference, implying that the resulting values of the weighted coherence can be regarded as a baseline for the effect of motor-driven movement per se. In contrast, in the active condition the changes in the EMG amplitude of the motor-driven hand resembled those observed for actively performed rhythmic wrist movements (as obtained for the right hand), and significantly larger coherence of the homologous muscle activity was observed.

For a proper evaluation of the adopted methodology it is relevant to note that the experiment actually involved a dual task paradigm, because in all conditions subjects were instructed to perform the required bimanual pattern and at the same time control the muscle activity in the driven arm. The additional cognitive load that is associated with performance of a secondary task may have augmented the intrinsic stability differences between in-phase and anti-phase coordination (Temprado et al. 1999). However, the results did not indicate a differential effect of the two secondary tasks (active vs. relaxed condition) on the stability difference between in-phase and antiphase (i.e., no Activity \times Pattern interactions were observed for SD_{ϕ}). From this we conclude that the additional cognitive load imposed by the secondary task was the same for the active and relaxed condition, and that the dual task paradigm did not confound the comparison between these conditions. In other words, we are confident that the observed differences between these conditions can be ascribed to the differences in muscle activity associated with these conditions, rather than differences in cognitive load. On the other hand, the dual task character of the present manipulations may explain why the present results regarding the SD_{ϕ} of in-phase and antiphase coordination agreed with those reported in the study of Stinear and Byblow (1999), in which an additional amplitude matching of the movements was required, but not with our previous (single task) experiment on kinesthetic tracking (Ridderikhoff et al. 2005b).

Muscle activity clearly had a beneficial effect on coordinative stability, as the variability of the relative phase was significantly smaller in the active condition than in the relaxed condition (Fig. 2b). In addition, the adopted mea-

asures related to the error correction processes underlying kinesthetic tracking, showing larger compensatory adjustments of the timing of the right hand in the active condition (R_{HC} and R_{FC} ; Fig. 3), indicated that kinesthetic afference was processed more effectively in this condition. Consequently, it seems unlikely that the muscle activity during kinesthetic tracking that we observed in our previous study (Ridderikhoff et al. 2005b) was merely a byproduct due to neural cross-talk.² However, in addition to these benefits of muscle activity, we also found that the absolute (and constant) errors in the mean relative phase were larger in the active condition than in the relaxed condition (Fig. 2a), indicating that the coordinative pattern was performed less accurately in the former condition. Thus, muscle activation during kinesthetic tracking resulted in more pronounced and proficient error corrections in bimanual timing, but these corrections appeared to be performed with respect to less accurate reference values.

In explaining this reduced accuracy in the active condition it proved essential to dissociate the temporal relations between the limbs observed at the level of neural control signals and those observed at the behavioral level, because these levels may involve separate reference signals. In the relaxed condition only the relative phasing at the behavioral level (kinematics) is available as reference for the error corrections. In contrast, the presence of a bilateral neural control signal in the active condition implies that the relative phase between the neural control signals (or motor outflow) may also be used as reference (e.g., by means of anticipation of the sensory consequences of the ongoing movement based on efference copies). Comparison of the constant errors at the two levels (Table 2) suggested an attraction toward the proper timing of the neural control signals, resulting in larger errors in the relative phase at the behavioral level (Fig. 7). This observation also revealed a discrepancy between the relative phases at the two levels, which resulted from an inadequate timing of the neural control signals of the motor-driven hand as explained in the next subsection.

This interpretation of the results underscores that bimanual coordination benefited from muscle activity during kinesthetic tracking because the bilateral motor commands were used (e.g., via efference copy) as a ref-

² Nevertheless, the differences between the active and the relaxed condition in terms of the range of motion and the associated EMG amplitudes of the right hand may indicate neural cross-talk influences (Cattaert et al. 1999; Ridderikhoff et al. 2005a; Swinnen 2002) and can be explained in two (not mutually exclusive) ways. The amplitudes may be increased in the active condition due to ‘motor’ overflow stemming from the left hand (Hoy et al. 2004). Alternatively, in the relaxed condition an amplitude reduction may have been associated with inhibition processes to avoid activation of the muscles of the driven (left) arm (Daffertshofer et al. 2005), i.e., to reduce the amount of overflow to the left hand.

erence signal for movement-elicited afference. The presence of this reference signal, which presumably allowed for prediction of the sensory consequences of the bimanual movement, resulted in more prominent error corrections, leading to a smaller variability of the relative phase in the active condition. Thus, the evidence suggested that an intimate sensorimotor integration, which has been proposed in the context of discrete goal-directed movements (e.g., Wolpert and Ghahramani 2000; Scott 2004), also underlies the coordination of rhythmic bimanual movements. In the context of the present study this interpretation can account for the observed effects of muscle activation on the stability as well as the accuracy of the relative phase.

Timing of the EMG activity in the motor-driven arm

Unlike the phase shifts between EMG and kinematics of the left (motor-driven) arm observed in the present study, the muscle activity observed during kinesthetic tracking in our previous study (Ridderikhoff et al. 2005b) was adequately timed with respect to the ongoing motor-driven movement. A possible explanation for this unexpected discrepancy between these two studies may be related to the instructions given to the subjects. In the active condition of the present study subjects were explicitly instructed to activate their muscles, whereas subjects did this spontaneously (i.e., without instruction) in our previous study. Given the instruction to activate the muscles as if moving along with the passive movement, subjects seemed to have aimed at generating contact forces that gave the impression that they were pushing or pulling the manipulandum in the correct direction. Comparison of the EMG amplitudes in the left (motor-driven) arm and the right (actively moving) arm (Fig. 5) indicated that this was accomplished by an earlier activation of the muscles in the left arm (relative to the ongoing movement) and an increase of the EMG amplitude (i.e., an increase of the muscle torque). These changes substantially increased the forces acting between the hand and the manipulandum in the direction of the ongoing movement. Note also that the EMG activity was minimal at the moments of peak excursion, i.e., when the movement changed direction (see Fig. 5). In other words, the results suggested that subjects in effect sought after the expected sensory consequences of moving something. This may be regarded as a misinterpretation of the instruction, because truly moving along requires the elimination of contact forces altogether.

Flexor–extensor differences during active rhythmic wrist movement

In addition to the effects of afference-based interlimb interactions (as reflected in the error corrections) the

flexion and extension phases were also affected by the unimanual control processes underlying the rhythmic movement of the (right) wrist itself. In this regard, an asymmetry was found in the correlations between successive flexion and extension half-cycles (R_{yy}), indicating that the durations of the flexion half-cycles were adapted more to changes in the duration of the extension half-cycle than vice versa (Fig. 4a). Studies on unilateral rhythmic movements have also reported an asymmetric relation between flexion and extension half-cycles in rhythmic finger movements (Balasubramaniam et al. 2004), and a more adequate temporal control of wrist flexion than wrist extension (Carson 1996; Carson and Riek 1998). An adaptive relation between the relative timing of FCR and ECR on the one hand and the resulting wrist movements on the other hand was also indicated by the analysis of the phase shifts between EMG and kinematics. Different phase shifts were obtained for FCR and ECR in the right hand but not in the left hand, in which timing of EMG and kinematics were unrelated. Such differences in the relative timing of FCR and ECR activity during rhythmic wrist movements have been reported before (Ridderikhoff et al. 2004), and may reflect adaptations to the different physiological properties of these muscles that would affect the movement trajectories unless compensated for. Furthermore, the EMG analysis revealed that the coherence between left and right ECR was larger than the coherence between left and right FCR, may be related to the finding that neural cross-talk effects were larger for extensor than for flexor muscles (Ridderikhoff et al. 2005a). These combined results point to a more independent control of the timing of FCR in the context of rhythmic wrist movement.

Conclusion

The present study revealed two characteristics of the error corrections based on the kinesthetically perceived relative phase that are relevant to the understanding of rhythmic bimanual coordination, and supplement the findings of our previous study on the sources of interlimb interaction involved in this type of task (Ridderikhoff et al. 2005b). First, the corrections were more effective during in-phase than during antiphase coordination, resulting in a smaller variability of the relative phase in the former condition. This effect may be attributable to differences in the kinesthetic perception of variability in in-phase and antiphase coordination (Wilson et al. 2003), and indicated that afference-based error corrections contribute to the well-known stability difference of these bimanual patterns (Kelso 1984; Swinnen 2002). Thus, although somatosensory feedback is not essential for the stability differences between in-phase and antiphase (Spencer et al. 2005), the

present study showed that afference-based error corrections augment the stability difference resulting from open-loop processes underlying the integrated timing of the efferent signals to both limbs (Ridderikhoff et al. 2005b). Second, the corrections (and, as a consequence, pattern stability) were enhanced if the muscles in the motor-driven arm were activated as if the limb was moving along with the motor. On the other hand, the accuracy of the relative phasing between the limbs was decreased in this situation, indicating that the corrections were based on a different reference signal than in the relaxed condition. The most likely explanation for these findings was that the bilateral neural control signal provided a reference for the evaluation of the kinesthetic afference, in the sense that on the basis of this signal the sensory consequences (of the bimanual movement pattern) could be anticipated. A closed-loop control process that exploits this kind of prediction is apparently more effective in terms of the stabilization of the relative phase. This result suggests an intimate relation between the integrated timing of the feedforward signals (underlying the bilateral activation pattern if both hands are moving actively) and the use of kinesthetic feedback in rhythmic bimanual coordination

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Appendix

The correlations reported in the main text (R_{FC} , R_{HC} , R_{xy} , and R_{yy}) are based on the covariances C_{FC} , C_{HC} , C_{xy} , and C_{yy} , respectively, which are defined in the following [Eqs. (A1), (A3), (A6), and (A5), respectively]. All covariances and correlations represent temporal relations between kinematic variables: the timing of peak flexion and extension. To obtain the correlations the covariances are divided by the product of the standard deviations of the two variables involved (i.e., normalized). Although correlations were analyzed in the present study, because these normalized measures provide an appropriate means to compare the temporal structure of the performance across various conditions, the formal relations between these correlations are more conveniently analyzed in terms of the underlying covariances. Furthermore, as mentioned in ‘‘Results’’, the effects observed could not be attributed to differences in the associated normalization factors.

Using the definitions of Fig. 1, the covariance of the signed error at peak flexion or extension and the duration of the next full cycle (C_{FC}^F and C_{FC}^E , respectively) is defined for in-phase coordination as

$$C_{FC}^p = \mathcal{N} \left\langle (\varepsilon_i^p - \langle \varepsilon^p \rangle) \left(\Delta t_{y,i}^p - \langle \Delta t_y^p \rangle \right) \right\rangle \quad (\text{A1})$$

where the superscript p indicates flexion (F) or extension (E), and $\langle \rangle$ represents the mean over all cycles $i = 1, 2, \dots, N$. The normalization constant $\mathcal{N} = N(N-1)^{-1}$ signifies that for (co)variances the sum is divided by the number of degrees of freedom ($N-1$) instead of N . To obtain a similar relation for antiphase coordination a different definition of the timing errors (ε_i) than shown in Fig. 1 should be used. For antiphase coordination, the timing error equals the difference in the timing of peak flexion of the right hand and peak extension of the left hand for C_{FC}^F , and the difference in the timing of peak extension of the right hand and peak flexion of the left hand for C_{FC}^E (cf. Ridderikhoff et al. 2005b). The consequences of this different definition for the partitioning of the covariance C_{FC} are addressed in relation to Eq. (A7).

Partitioning of C_{FC} is performed to elucidate the relation between C_{FC} , C_{HC} , C_{xy} , and C_{yy} (and between the associated correlations used in the analyses). In the following this is illustrated for in-phase coordination by expressing Eq. (A1) in terms of the durations of half-cycles as

$$C_{FC}^p = C_{HC}^q + \mathcal{N} \left\langle (\varepsilon_i^p - \langle \varepsilon^p \rangle) \left(\delta t_{y,i}^p - \langle \delta t_y^p \rangle \right) \right\rangle \quad (\text{A2})$$

where indices p and q refer to either flexion (F) or extension (E), with $p \neq q$. C_{HC}^q is the covariance of the error at peak flexion or extension and the duration of the next half-cycle. This covariance can be defined generically as

$$C_{HC}^q = \mathcal{N} \left\langle (\varepsilon_i^p - \langle \varepsilon^p \rangle) \left(\delta t_{y,i}^q - \langle \delta t_y^q \rangle \right) \right\rangle \quad (\text{A3})$$

where indices p and q refer to either flexion (F) or extension (E), with $p \neq q$. The second term on the right hand side (RHS) of (A2) can be expanded further using the following relation between the duration of the half-cycles and the signed errors: $\delta t_{y,i}^q + \varepsilon_i^p = \delta t_{x,i}^q + \varepsilon_i^q$ (see Fig. 1). Substitution of ε_i^p in (A2) yields

$$C_{FC}^p = C_{HC}^q + C_{HC}^p - C_{yy}^{q \rightarrow p} + C_{xy}^{q \rightarrow p} \quad (\text{A4})$$

for in-phase coordination. The third term on the RHS of Eq. (A4) is the (‘‘within-hand’’) covariance of the durations of successive half-cycles of the right hand (y), which is defined as

$$C_{yy}^{p \rightarrow q} = \mathcal{N} \left\langle \left(\delta t_{y,i}^p - \langle \delta t_y^p \rangle \right) \left(\delta t_{y,i}^q - \langle \delta t_y^q \rangle \right) \right\rangle \quad (\text{A5})$$

The fourth term on the RHS of Eq. (A4) is the (‘‘between-hands’’) covariance of the duration of a half-cycle of the left hand (x) and the following half-cycle of the right hand (y) defined as

$$C_{xy}^{p \rightarrow q} = \mathcal{N} \left\langle \left(\delta t_{x,i}^p - \langle \delta t_x^p \rangle \right) \left(\delta t_{y,i}^q - \langle \delta t_y^q \rangle \right) \right\rangle \quad (\text{A6})$$

Equation (A4) is valid for in-phase coordination. Using the same partitioning with the adapted definition of the signed error we obtain for antiphase coordination:

$$C_{\text{FC}}^p = C_{\text{HC}}^q + C_{\text{HC}}^p - C_{yy}^{q \rightarrow p} + C_{xy}^{p \rightarrow p} \quad (\text{A7})$$

Interestingly, examination of (A4) as well as (A7) shows that the partitioning of C_{FC}^F and C_{FC}^E always contains the sum $C_{\text{HC}}^E + C_{\text{HC}}^F$. Thus, differences between flexion and extension for R_{FC} cannot be attributed to the covariances underlying R_{HC} . Instead these differences should be accounted for in terms of the covariances associated with the “within-hand” and “between-hands” correlations (R_{yy} and R_{xy} , respectively). As explained in “Materials and methods”, these correlations are not directly related to the (correction of) relative phasing errors, but reflect dependencies between the error corrections in successive half-cycles.

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