

Arm Motion Coupling During Locomotion-Like Actions: An Experimental Study and a Dynamic Model

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We studied the coordination of arm movements in standing persons who performed an out-of-phase arm-swinging task while stepping in place or while standing. The subjects were instructed to stop one of the arms in response to an auditory signal while trying to keep the rest of the movement pattern unchanged. A significant increase was observed in the amplitude of the arm that continued swinging under both the stepping and standing conditions. This increase was similar between the right and left arms. A dynamic model was developed including two coupled nonlinear van der Pol oscillators. We assumed that stopping an arm did not eliminate the coupling but introduced a new constraint. Within the model, superposition of two factors, a command to stop the ongoing movement of one arm and the coupling between the two oscillators, has been able to account for the observed effects. The model makes predictions for future experiments.

Keywords: locomotion, dynamic system, coupling

When humans walk, they typically swing the arms at the frequency of leg motion. Arm swinging during human locomotion has been viewed as a consequence of coupling between hypothetical pattern generators for the lower and upper extremities (Donker et al. 2001; Ustinova et al. 2006). Several recent studies have supported the view on common neural control of arm and leg movements during rhythmic human actions (Ustinova et al. 2006; Zehr et al. 2008). This view has also been supported by a study of the effects of a one-arm restraint during walking (Marks 1997). This study revealed a trend toward greater thoracic rotation on the unrestrained side and altered angular velocity profiles for all the upper and lower limb joints and the trunk.

The purpose of arm swinging during locomotion has typically been viewed as directed at stabilizing the total moment of force acting about the vertical body axis. In particular, a recent study of walking with and without arm swinging showed that the variable that differed most between the two conditions was the free vertical moment between the feet and ground (Umberger 2008).

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Stable patterns of modulation of the upper and lower extremity muscles are also observed when the subjects swing their arms rhythmically while standing (Abe & Yamada 2001). These patterns have been discussed as related to stabilization of the moment of force acting about the vertical body axis (Danna-Dos-Santos et al. 2009). Another study has shown that, when standing subjects swing the arms as if they are walking, axial trunk muscles are sequentially activated by a motor command running along the spinal cord (de Seze et al. 2008). It is not known whether rhythmic leg movement is necessary for the typical coupling effects between the two arms.

Note, however, that the rhythmic arm movement during locomotion is not obligatory, and walking is possible without visible arm swinging, for example with a mug of hot coffee in one of the hands or while carrying a load with both hands. These observations suggest that a voluntary command can override the hypothetical common control of the arm and leg movements during walking. The main purpose of our study has been to explore the interactions between rhythmic motor patterns produced by a hypothetical neural oscillator and a voluntary motor command unrelated to the ongoing rhythmic action, such as stopping one of the arms voluntarily. Our primary hypothesis was that effects of the command for the discrete voluntary action on the rhythmic action of the other arm could be described with a new constraint on the neural oscillator without a change in the coupling between the arms. In line with this prediction, we developed a simple dynamic model motivated by the Haken-Kelso-Bunz model (Haken et al. 1985) to account for the observed effects on the movement amplitude of the arm that continued to sway.

An increase in the amplitude of an arm's movement after the other arm stopped would make sense as the means to compensate for the lack of contribution of the stopped arm to the moment of force about the vertical body axis. Note, however, that this argument fails if the subject performs rhythmic arm movements during standing, not during stepping. To explore the importance of rhythmic leg movements for this effect, the experiment was performed with and without stepping in place.

Methods

Subjects

Eight healthy subjects, 4 females and 4 males, mean weight 64.6 ± 13.2 kg (mean \pm *SD*), mean age 26.9 ± 3.5 years and mean height 1.70 ± 0.081 m participated in the experiment. All the subjects were healthy, without any known neurological, muscular or orthopedic disorder. All the subjects were right-handed based on their preferential hand usage during writing and eating. The subjects gave informed consent based on the procedures approved by the Office for Research Protection of The Pennsylvania State University.

Apparatus

A four-camera ProReflex motion analysis system was used to capture the position of six passive reflective markers at 240 Hz. The spherical 26-mm markers were attached to the skin with double-sided tape. The markers were positioned on the superficial bony prominences to reduce the effect of skin movement. They were

placed on both sides of the body over the shoulder (in the middle part of acromion), elbow (lateral epicondyle), and wrist (styloid process of ulna) joints. The system was calibrated before every testing session.

Procedures

The experiment involved several series with arm movements performed either while standing (the STAND condition) or while marching in place (the STEP condition) on the AMTI-7 force plate. In all experiments, the subjects were instructed to look at the stationary target placed 1.2 m in front of the subject at the eye level. The feet were kept parallel and apart 15 cm. This foot position was marked on the top of the force plate and reproduced across all the trials.

The subjects were instructed to perform alternating rhythmic arm movements imitating fast walking (similar to race walking). The subjects were allowed to use their preferred style of arm movement while trying to move the hands between two nominal targets positioned at the face and hip levels. The targets were used only to suggest an amplitude of arm movement. We did not want the subjects to focus on being exactly on the targets because this could interfere with spontaneous changes in arm movement after the other arm stopped. By instruction, the trajectory and frequency of arm movements had to be similar across all series. Although the range of motion in each joint was not specified, on average, the shoulder joint peak-to-peak excursion was approximately 40–50 degrees while the elbow joint peak-to-peak excursion was approximately 90 degrees. There were no visible movements in the wrist joint and in any of the hand joints. The fingers were extended.

Before the main series, a comfortable natural frequency of arm movements was defined when the subjects marched in place at their preferred rhythm. In all subjects, the comfortable frequency was between 0.8 and 0.9 Hz. Further, eight series of trials were run that differed in the main task (STAND or STEP), the frequency of movement (comfortable or fast, defined as the frequency 20% higher than the comfortable one), and the instructed arm (right or left, see the next paragraph). Before data collection, the subjects performed 2–3 trials under both comfortable and fast frequencies. The practice time was about 5–6 min.

In the main experiment, every trial began with the metronome pacing the subject at the required frequency. After 6 s (4–6 cycles), the metronome was turned off, and the subject continued moving at the same pace for the next 8–10 s, until an audio signal (a “beep”) was given. The subject was instructed to stop moving one of the arms immediately after the beep and to continue performing the task naturally (moving the other hand and marching in place or standing) during 8–10 s, until the end of the trial signal was given. Before each set of trials, the subject was instructed which of the arms, right or left, had to be stopped. The instructed arm had to be stopped within the cycle immediately following the beep and remain vertical, along the trunk, while touching lightly the body (thigh). The beep was generated by the computer at random times. This was done to avoid linking the effects of the beep to a particular motion phase.

The duration of each trial was 24 s. There were 8 blocks of 15 trials corresponding to the $2 \times 2 \times 2$ (Frequency \times Task \times Arm) design. The order of conditions was balanced across subjects. There were 10-s intervals between trials within a block and rest periods of about 1–2 min between blocks; fatigue was not an issue.

Data Processing

Qualisys software was used to obtain 3-dimensional coordinates of each marker, which were then exported to Matlab for further analysis. At the first step, the trials that lost markers within a 7-s interval around the beep were rejected (about 14.6% of the trials). In each accepted trial, each marker coordinate was initially filtered with a 7-point median filter and then with a low-pass fourth order Butterworth filter with the cut-off frequency of 2 Hz. Such double filtration procedure was selected to minimize the influence of noise spikes in the marker coordinates on the estimation of the minima and maxima in the angle profiles (see below). To make sure that the filtering did not exert major effects on the kinematic data, we performed a pilot analysis with filtering at 5 Hz. The differences between the two filtering procedures for all the outcome measures were always under 2%. The marker coordinates were then projected on the XZ plane, which corresponded to a sagittal plane of the body. The arm angle (α_{ARM}) was defined as the angle between the vertical direction and the line connecting the projections of the shoulder and wrist markers on the XZ plane. An increase in α_{ARM} corresponded to the hand movement forward.

The moment of stopping the instructed arm, t_{STOP} was defined as the time, within 3 s after the beep, when the phase trajectory of α_{ARM} first entered a rectangle centered at the average value of the trajectory with the side lengths equal to 1.5 median values of α_{ARM} and its derivative during the cycles after the beep (see Figure 1). This criterion was selected based on several pilot tests as the one leading to most consistent results.

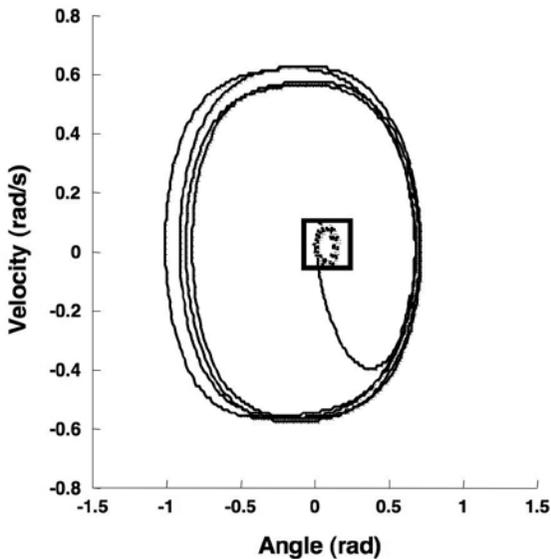


Figure 1 — A typical phase portrait of arm movement stopped voluntarily at some time in response to the auditory signal. The gray line shows the trajectory before the stop. The small rectangle shows the criterion used to define the time of arm stop. The moment of the hand stop was identified as the moment of the first entrance of the trajectory into the rectangle. There was always a small residual arm rhythmic motion.

The α_{ARM} trajectory was split into half-cycles defined as the time intervals between pairs of local maxima and minima of α_{ARM} . For the arm that continued to move (addressed further as the free arm), the average amplitude and duration of six half-cycles preceding t_{STOP} (excluding the half-cycle when t_{STOP} occurred) and of six half-cycles following t_{STOP} were computed. The amplitude of a half-cycle was defined as the absolute difference between the two consecutive extreme values of α_{ARM} .

Force platform data were used to quantify peak-to-peak changes in the moment of force about the vertical body axis (M_Z). The peak-to-peak values were computed for each cycle and then averaged across cycles within each condition for each subject, separately for the cycles with both arms swinging and after one of the arms stopped.

The Mathematical Model

Each arm motion was modeled with a single Van der Pol oscillator:

$$\begin{aligned} \ddot{x}_1 + v_1 \dot{x}_1 \left((x_1^2 + \dot{x}_1^2 / \omega_1^2) - A_1^2 \right) + \omega_1^2 x_1 &= f_1(x_1, \dot{x}_1, x_2, \dot{x}_2) \\ \ddot{x}_2 + v_2 \dot{x}_2 \left((x_2^2 + \dot{x}_2^2 / \omega_2^2) - A_2^2 \right) + \omega_2^2 x_2 &= f_2(x_1, \dot{x}_1, x_2, \dot{x}_2) \end{aligned} \quad (1)$$

Here x_1 and x_2 are α_{ARM} angles of the two upper extremities, ω_1 and ω_2 are prescribed frequencies and A_1 and A_2 are amplitudes parameters. Parameters v_1 and v_2 determine the strength of mechanisms stabilizing the desired oscillatory pattern.

Without the coupling functions f_1 and f_2 , each system would oscillate with its frequency ω and amplitude A . The coupling functions f_1 and f_2 lead to phase synchronization of the limbs, in particular making antiphase oscillation of x_1 and x_2 stable. Moreover, the functions f_1 and f_2 must be essentially symmetrical with respect to x_1 and x_2 , such that stopping the left hand would lead to qualitatively the same effect in the right hand, as stopping the right hand would do for the left hand motion. For these reasons we used the coupling functions borrowed from the Haken-Kelso-Bunz (HKB) model (Haken et al. 1985). We simplified these functions by reducing the number of free parameters to a minimum sufficient to account for the experimentally observed behavior:

$$\begin{aligned} f_1(x_1, \dot{x}_1, x_2, \dot{x}_2) &= -b_1 \dot{x}_1 (x_1 - x_2)^2 \\ f_2(x_1, \dot{x}_1, x_2, \dot{x}_2) &= -b_2 \dot{x}_2 (x_2 - x_1)^2 \end{aligned} \quad (2)$$

Here parameters b_1 , and b_2 determine the properties of the coupling between the two arms.

Different values of ω_1 and ω_2 in Eq. (1) may lead to significant desynchronization (see Fuchs et al. 1996) unless additional mechanisms are involved. Since including such mechanisms would complicate the model, we assumed that the prescribed frequencies are set by the CNS to equal values, $\omega_1 = \omega_2 = \omega$. All other parameters were allowed to differ for the two limbs

One can give a simple interpretation of the model. The CNS assigns a preferred frequency ω and amplitudes A_1, A_2 of the arm oscillations. Stability of the antiphase relationship between the two arms is defined by parameters b_1 and b_2 . The presence of the coupling functions influences amplitudes of the arm movements, such that actual amplitudes differ from the prescribed ones and depend on b_1 and b_2 .

We assumed that stopping one arm does not cancel the coupling function in Eqs (2) and thus there are additional mechanisms that keep the instructed arm static. We modeled the influence of those mechanisms by introducing an additional constraint $x_1 = 0$ (or $x_2 = 0$) into the system 2.

Statistical Analysis

For each task, the data were averaged across all trails for each subject separately. Standard methods of parametric statistics were used. Analysis of variance (ANOVA) with repeated measures was applied to the angular displacement and duration of each half-cycle. Normalized change in the angular displacement (ΔA , in %) of an arm after the other arm stopped moving was calculated as: $[(A_{\text{POST}} - A_{\text{PRE}}) / A_{\text{PRE}}] \cdot 100\%$. The ANOVA factors were: *Period* (before and after arm stop), *Task* (stepping and standing), *Side* (right and left), and *Speed* (comfortable and fast). A random factor *Subject* was used, but its effects are not reported. In particular, we used ANOVA to answer the following questions: Does self-termination of a rhythmic arm movement affect amplitude and frequency of the ongoing movement of the other hand? Does this effect differ between the right and left hands, between comfortable and fast arm movements, and between the stepping and standing tasks? Tukey's pairwise comparisons were used to analyze significant effects. Analyses of the shoulder, elbow and whole-arm data produced qualitatively and quantitatively similar results. Hence, in the following section we present only the whole-arm data, not analysis of individual joint motion.

Results

Steady-State Arm Motion

The comfortable frequencies of the arm movements during stepping and standing ranged from 0.8 to 0.9 Hz, 0.863 ± 0.02 Hz (mean \pm SE). Under the 'fast' instruction, the arm frequency ranged from 0.9 to 1.083 Hz (1.007 ± 0.025 Hz). In most subjects, the frequency of the metronome paced arm movements differed from that of the movements performed after the metronome had been turned off by 0.5–3%. In two subjects, the difference was higher (lower by 15–20%) and this effect was systematically reproduced across conditions.

The subjects were free to select their particular style of performing arm movements. As a result, relative involvement of the joint excursions differed broadly across the subjects, while the motion of the endpoint was much more consistent. The whole-arm motion amplitude was, on average, $57.2^\circ \pm 2.61^\circ$ for the right arm, and $62.8^\circ \pm 4.14^\circ$ for the left arm.

Typical individual data illustrating changes in the magnitude and duration of the cycle are shown in Figure 2. The average across trials time series are shown as a solid line, with standard deviations shown with dotted lines. Panel A shows data for the STAND task with the right hand continuing the action after the left hand stopped, while panel B shows similar data for the STEP task.

During the initial steady-state, the movement cycle frequency was 0.901 ± 0.03 Hz for the comfortable speed, and 1.042 ± 0.04 Hz for the fast speed. There were no differences in stepping frequency between the STEP and STAND tasks

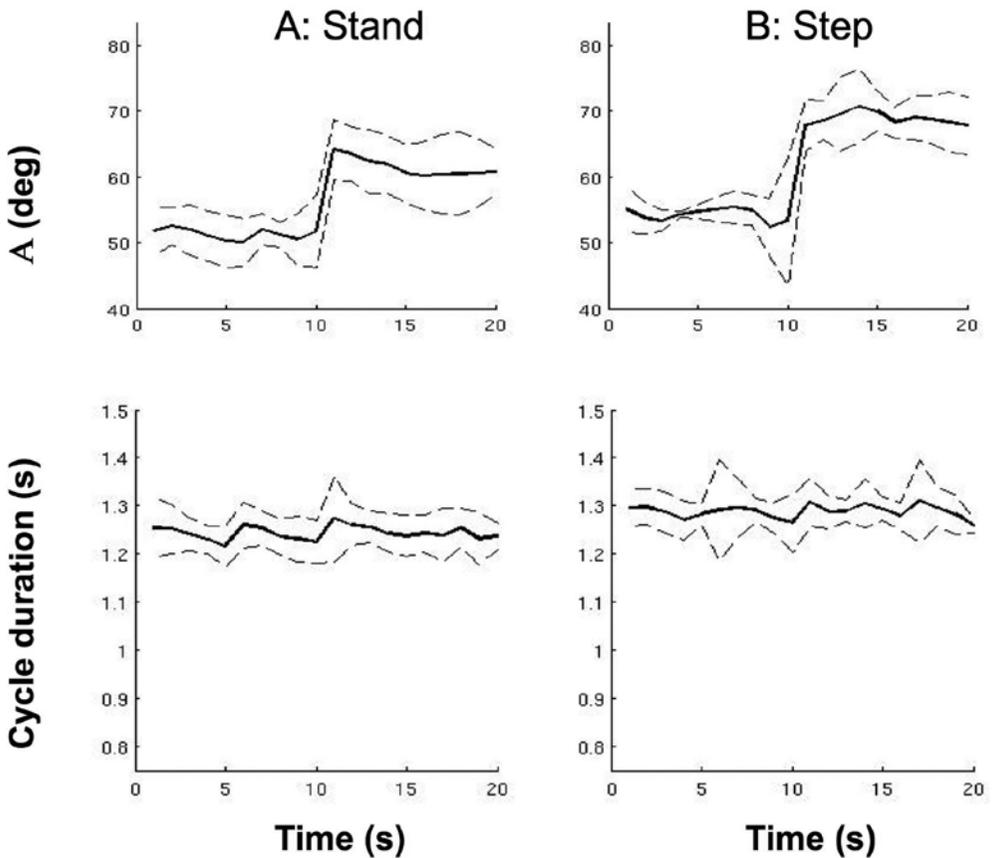


Figure 2 — An illustration of changes in the cycle amplitude (top panels) and duration (bottom panels) after stopping the contralateral arm. The data are shown for the standing (A) and stepping (B) tasks performed by a typical subject at a comfortable speed. The left arm stopped at the time 0 s. Note the increase in the right arm movement magnitude without a change in the cycle duration. Data averaged across trails with standard deviations are shown.

and between the right and left arms. A three-way ANOVA with factors *Task*, *Speed*, and *Side* confirmed a significant effect of *Speed* only ($F_{[1,52]} = 14.04$; $p < .001$) with no significant interactions.

The amplitude of arm motion (A) differed significantly between the STEP and STAND tasks: for the STEP task, it was $57.06^\circ \pm 3.19^\circ$, and for the STAND task, it was $62.93^\circ \pm 3.70^\circ$. This difference was smaller for the left arm (about 7.4%), while it was about 13.6% for the right arm. A three-way ANOVA with factors *Task*, *Speed*, and *Side* showed significant effects of two factors, *Task* ($F_{[1,52]} = 5.45$; $p < .05$) and *Side* ($F_{[1,52]} = 4.99$; $p < .05$) with no significant effect of *Speed* and no significant interactions.

Free Moving Arm: Comparison of Pre- and Post-STOP Cycles

After the voluntary self-termination of one arm movement, the continuing arm showed a 10–30% increase in its amplitude, A as compared with the pre-STOP amplitude. This effect was seen in all the subjects, for both arms, during both STEP and STAND tasks, and under both comfortable and fast speeds. The data averaged across subjects are presented in Figure 3.

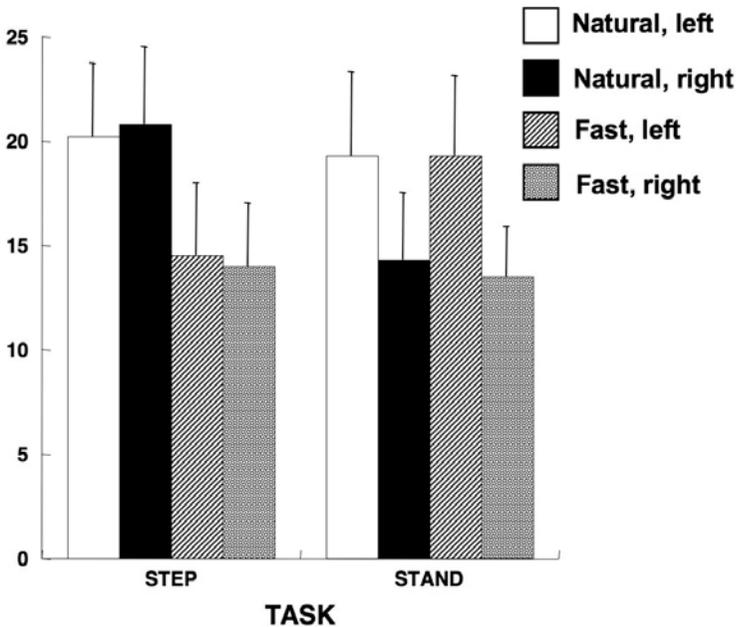


Figure 3 — An increase in the amplitude of arm movement after the contralateral arm stopped swinging. The data in percent to the prestop arm amplitude are presented for both natural (two left columns in each cluster, white—left arm, black—right arm) and fast (two right columns in each cluster, striped—left arm, dotted—right arm) speeds, and for the stepping and standing tasks. Data averaged across subjects with standard error bars across subjects are shown.

The increase in A (ΔA) between the pre-STOP and post-STOP data varied across subjects from 8% to 24%; on average it was $16.9\% \pm 1.08\%$. Figure 3 shows averaged across subjects data for the STEP and STAND tasks at both speeds.

A four-way ANOVA with the factors *Period*, *Task*, *Side*, and *Speed* on A showed significant effects of *Period* ($F_{[1,115]} = 31.32$; $p < .001$), *Task* ($F_{[1,115]} = 13.00$; $p < .001$), and *Side* ($F_{[1,115]} = 14.59$; $p < .001$) without an effect of *Speed* and without significant interactions. The main effects reflected higher A after the stop as compared with before the stop, during standing as compared with stepping, and in the left arm as compared with the right arm.

Similar analysis of the cycle duration showed only a significant effect of *Task* ($F_{[1,116]} = 9.8$, $p < .01$). On average, the arm cycle duration during stepping was

about 5% lower than during standing. There were no significant effects of other factors and no interactions.

We quantified the amplitude of forward-backward motion of the shoulder marker before and after the STOP. Across conditions, there was a small decrease (nonsignificant) in this parameter from 3.73 ± 0.24 cm to 3.28 ± 0.19 cm.

Peak-to-peak changes in the moment of force about the vertical body axis (M_Z) within the cycle were quantified for each condition and each subject for the STAND task. There were no differences in this index between trials with the right arm stop and left arm stop. Assuming that the contributions of each arm's movement to M_Z variation were equal, we compared 50% of peak-to-peak M_Z pre-STOP to total peak-to-peak M_Z post-STOP. On average, 50% of peak-to-peak changes of M_Z pre-STOP were 7.63 ± 0.88 and 8.38 ± 1.29 Nm for the natural and fast movements respectively. After STOP, these values increased to 10.57 ± 1.36 and 10.80 ± 1.66 Nm. The increase in peak-to-peak M_Z produced by one arm swinging was, on average, 36%. This increase was significant as confirmed by a two-way ANOVA that showed the effect of *Period* ($F_{[1,15]} > 13.0$; $p < .01$).

The Model

The model (see Eqs. (2) in Methods) was capable of producing cyclic changes of the variables x_1 and x_2 , which we associated with the left and right arm angles respectively. The frequency of the cyclic motion of the model is equal to ω . An example of the model output is given in Figure 4. Note that the amplitude of movement depends on parameters b_1 and b_2 of the coupling functions. In the absence of coupling, when $b_1 = b_2 = 0$, the amplitude is equal to $2A_1$ (or $2A_2$). Note, that here we define amplitude as peak-to-peak distance, instead of half of peak-to-peak distance, which is a conventional definition in the theory of oscillations and is applicable to sinusoidal signals only. Since the hand stop was modeled by the constraint $x_1 = 0$ (or $x_2 = 0$), b_1 and b_2 were never zero. As a result, when one of the hands stopped, the amplitude of the other hand's motion was not equal to $2A_1$ (or $2A_2$).

In the absence of the coupling function the cyclic movements are stable for positive values of the damping parameter ν and the time of the disturbance compensation is roughly inversely proportional to the value of ν . The current study does not aim to present a detailed analysis of Eqs. (1) and (2) and thus we do not investigate here the stability conditions in presence of the coupling functions.

The existence of a stable solution corresponding to antiphase motion of the two arms (x_1 and x_2) is guaranteed by the coupling function with $b_1 > 0$ and $b_2 > 0$. The numeric simulations show that the coupling function stabilizes antiphase movements and makes in-phase coordination unstable. However, depending on the strength of the coupling (parameters b_1 and b_2) the time required to converge to antiphase trajectory may differ. Similar to ν , b_1 and b_2 determine how quickly a phase disturbance will decay. The time of disturbance compensation is roughly inversely proportional to the values of b_1 and b_2 .

The model parameters were tuned to describe the experimentally observed behavior. We set the frequency parameter ω equal to the average experimental value for the normal speed in the STAND condition, $\omega = 2\pi/1.12$ Hz. The dissipation parameter ν was arbitrarily set to 10 Hz. For this value, any deviation from the cyclic pattern decays almost completely within 300 ms.

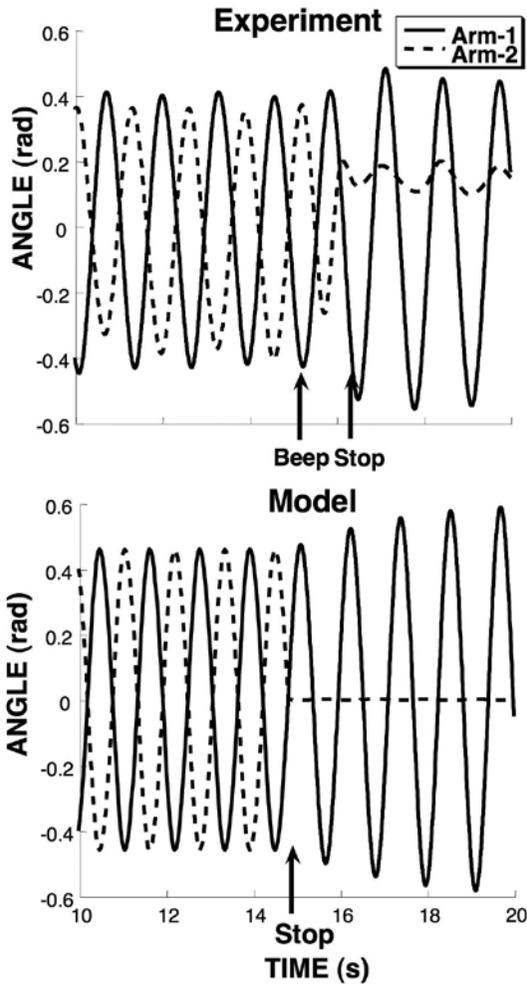


Figure 4 — Results of the simulation. A: a representative example of the arm sway trajectory. The arrows show the beep and stop moments. B: the model output with the parameters defined using the average experimental values (see the text). The arrow shows the time of introducing the constraint $x_2 = 0$. Note the increase in the amplitude of the continuing arm motion in both panels.

The amplitude parameters A_1 and A_2 were set to the average values of the arm amplitude (A) after the other hand stopped. Then, the coupling parameters b_1 and b_2 were tuned to achieve approximately the percentage of the amplitude increase for each arm that was observed in the experiments. Finally, all four parameters (A_1 , A_2 , b_1 , and b_2) were simultaneously corrected so that both pre- and poststop values for the hand trajectory were close to the experimentally observed ones. The values for the parameters were: $A_1 = 42.4^\circ$, $A_2 = 36.4^\circ$, $b_1 = 5.8$ Hz, $b_2 = 3.2$ Hz.

The resulting arm amplitudes before stop were 68.5° (left), 62.0° (right), and after stop they were 79.0° (left), 70.4° (right).

We checked the influence of movement speed on the model behavior by setting the frequency $\omega = 2\pi/1.00$ Hz, which corresponds to the average experimental frequency in the fast condition. The other parameters of the model were left unchanged. There was a slight increase of the pre- and poststop amplitudes of x_1 and x_2 . The increase was less than 1° , which may be considered minor.

In the current study, we modeled the stop of one arm by introducing additional constraints. At the first glance it seems more logical to model the stop simply by setting corresponding amplitude parameter to zero ($A_1 = 0$ or $A_2 = 0$). Indeed, the latter leads to decay of one hand's oscillation within about 10 s and causes a similar increase in the amplitude of the other hand as the complete stop does. However, in the experiment the hand stopped within a second or two after the beep.

Discussion

Our experiments have shown strong coupling effects between the two arms. Indeed, when the subjects stopped moving one of the arms, the amplitude of the other arm movement increased significantly. This effect was nearly symmetrical between the left and right arms. It was similar in magnitude in the tasks that did and did not involve simultaneous rhythmic leg movement (marching in place). We were able to model the effect using a simple dynamic model with two coupled nonlinear oscillators, similar to the one suggested by Haken et al. (1985). Further, we discuss implications of these results for the arm coordination in rhythmic tasks and make predictions for future experiments.

Implications for Arm Coordination

Although humans can use the two arms relatively independently across a variety of everyday activities, two dominant patterns have been described in the literature, in-phase and antiphase. A general tendency toward symmetrical (in-phase) arm actions has been described for a variety of bimanual tasks that did not involve legs (Walter & Swinnen 1990; Swinnen et al. 1991; Carson et al. 2007). On the other hand, locomotion (walking and running) is typically associated with an antiphase pattern of arm movement.

One possible reason for the alternating arm movements during walking is to compensate for the time-varying moment of force acting about the vertical axis of the body due to the alternating stepping leg movements (cf. Umberger 2008). In particular, this may facilitate constancy of visual perception by mitigating the effects of the asymmetrical leg movements on head trajectory. Our data are partly consistent with this interpretation. Indeed, stopping one arm naturally eliminated the contribution of its motion on the overall moment of force about the vertical body axis. The increased amplitude of the other arm swing may be seen as (partly) compensating for this effect. This would be beneficial when the subjects performed the task while marching in place. However, we observed similar effects when the subjects performed the same task while standing. In those conditions, the arm movements contributed to the nonzero total moment of the force about the vertical body axis (M_z), not mitigated effects of leg motion on this moment of force, and an

increase in the amplitude of the motion of the continuing arm could not be seen as reducing this moment of force. Moreover, when we compared the estimated contribution of one arm's movement to the M_z peak-to-peak amplitude before and after the other arm stopped, the results showed significantly higher values after the stop.

The similar observations under the stepping and standing conditions question the importance of locomotion for the observed effects. Many authors have discussed the alternating arm movement patterns in standing persons as resulting from coupling with the leg movements (Kaminski 2007; Kawashima et al. 2008; Zehr et al. 2008). Our experiments show that similar arm coupling may take place in the absence of a locomotor-like leg activity. It is possible that the alternating arm swinging is so tightly associated with locomotion that the neural coupling remains unchanged even if it loses its mechanical importance (in the absence of stepping). This conclusion is in line with a few studies of arm swinging by standing persons (Abe & Yamada 2001; Baldissera et al. 2008).

We observed only minor differences between the left and right arm in the parameters of the swinging motion and the effects of the other arm stopping. The left arm tended to swing at a lower amplitude (in contrast to an earlier report by Kuitz-Buschbeck et al. 2008). However, the increase in the movement amplitude, associated with stopping the other arm, was similar in the two arms.

In a recent paper, Ustinova and colleagues (2006) have suggested that a central generator controls both arms as a coherent unit by producing transitions between its steady states. Following a similar reasoning, we developed a simple dynamic model controlled by only a few parameters supplied by a hypothetical neural controller and discussed in the next section.

The Model and Its Fit to the Data

Patterns of bilateral movements of symmetrical effectors have been studied using dynamic models, commonly consisting of two (or more) coupled nonlinear oscillators (reviewed in Schönér & Kelso 1988; Kelso 1995). One of the most commonly cited models is the so-called HKB model (Haken et al. 1985). This model was developed to account for certain features of bilateral rhythmic actions (for example, bilateral finger or hand actions, Kelso et al. 1979, 1981) such as phase transitions and critical slowing observed with changes in the frequency of the action. Relatively little attention was paid to possible changes in the amplitude of action of the individual effectors (Swinnen et al. 2001).

In the proposed model, Van der Pol oscillators describe essential dynamics of the arm swinging, i.e., the summed effect of functioning of a hypothetical neural network coupled to the dynamical properties of the arm. Though the arm movement can be considered as a consequence of many dynamical processes, the observed behavior (that is, nearly harmonic oscillation of the arm) confirms that, among all those processes, there is one with characteristic time of actual arm swinging, while the characteristic times of the others processes are either significantly larger or smaller. Thus, though we cannot provide a better explanation of why the arm movement is cyclic, we can use a simplified mathematical model, which captures the main properties of the process: (i) its periodic nature, (ii) stability of its amplitude and frequency. It can be clearly seen that, at least within some range of parameters, van der Pol oscillator has the desired properties.

At the next step of building the model we introduced a coupling function with the following properties: (i) antiphase oscillations are stable, (ii) in-phase oscillations are unstable, (iii) the presence of the coupling function does not significantly change the oscillators' dynamics, (iv) the number of parameters of the coupling function is such that they can be identified based on the experimental data we collect.

The model we use in the current study represents a simplified version of the HKB model. In particular, we reduced the number of parameters of the HKB-model to a minimal value sufficient to guarantee the stability of antiphase movements of the arms and to describe the experimentally observed effects of the left/right arm stop. There are six parameters in the model: ω , ν , A_1 , A_2 , b_1 , b_2 , which were estimated based on five experimentally found values: step frequency, left and right arm amplitudes before and after the stop of the opposite arm. To deal with the problem of redundancy of parameter estimation we arbitrarily assigned to ν such a value that deviations of the rhythmic arm movements almost totally decayed within 300 ms (consistent with the quickest arm stop across our experiments). Based on the numeric estimations we assumed that, for a fixed value of ν , there is a unique set of the other model parameters consistent with the experimental data.

The model could be further simplified by assuming $A_1 = A_2$ and $b_1 = b_2$. However, in this case, the model is unable to describe the observed small asymmetry of the arm stop effect. According to the model, the higher relative amplitude increase in the left arm points at stronger phase stabilizing mechanisms in this arm. The latter may result in lower independence of the left arm as compared with the right arm that seems natural for the right-handed population participating in the study.

Note that we fixed the model parameters at values that allowed the model to fit the average experimental data for the STAND condition, when arm swing was performed at the normal frequency.

The introduced coupling function may be viewed as a first approximation. Unfortunately, we see no way to make a more precise approximation without introducing parameters whose values we cannot estimate based on the experimental data. We believe that, to obtain a second approximation of the coupling function, one should discover and quantify additional properties of the arm interaction during locomotion. We would like to emphasize that the proposed coupling function is far from unique. For example, a change of the power "2" to any odd number does not lead to any qualitative change in behavior.

At this stage, we cannot offer a physiological interpretation of the model. In our model, each van der Pohl oscillator describes the dynamic behavior of a limb, which reflects joint dynamics of the arm and of a corresponding central pattern generator (CPG) that controls it. That is, each oscillator reflects behavior of a complex neuro-mechanical system. We assume here that cyclic multilimb actions, such as locomotion, are controlled by hierarchies of CPGs (McCrae, Rybak 2008) and that each of the oscillators reflects the interactions of one of the CPGs with the mechanics of the effector it controls.

New Predictions of the Model

The model suggested in our paper makes predictions that go beyond the described experiments. In particular, the nature of the coupling function is such that a decrease in the oscillation amplitude of one hand leads to an increase in the oscillation

amplitude of the other hand. We explored the model behavior under a different “instruction”: A voluntary increase in the oscillation amplitude of one of the arms. Simulations were run using the same set of parameters and $\omega=2\pi/1.12$ Hz (which corresponds to the arm frequency under the normal speed condition in the described experiment). To model a voluntary increase in the movement amplitude of one of the arms, the amplitude parameter of that arm (A_1 or A_2) was increased by 50%. We found that an increase of the right arm A parameter by 50% led to an about 13% drop in the left arm movement amplitude. A similar increase of the left arm A parameter caused a 12% decrease in the right arm movement amplitude. It must be emphasized that these results were obtained for the model parameters fitting average experimental data in the described experiments. We plan to run experiments that would validate or disprove these predictions.

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References

- Abe, M., & Yamada, N. (2001). Postural coordination patterns associated with the swinging frequency of arms. *Experimental Brain Research*, *139*, 120–125.
- Baldissera, F., Rota, V., & Roberto Esposti, R. (2008). Anticipatory postural adjustments in arm muscles associated with movements of the contralateral limb and their possible role in interlimb coordination. *Experimental Brain Research*, *185*, 63–74.
- Carson, R.G., Smethurst, C.J., Oytam, Y., & de Rugy, A. (2007). Postural context alters the stability of bimanual coordination by modulating the crossed excitability of corticospinal pathways. *Journal of Neurophysiology*, *97*, 2016–2023.
- Danna-Dos-Santos, A., Shapkova, E., Shapkova, A., Degani, A., & Latash, M.L. (2009). Postural control during upper body locomotor-like movements: similar synergies based on dissimilar muscle modes. *Experimental Brain Research*, *193*, 565–579.
- Donker, S.F., Beek, P.J., Wagenaar, R.C., & Mulder, T. (2001). Coordination between arm and leg movements during locomotion. *Journal of Motor Behavior*, *33*, 86–102.
- Fuchs, A., Jirsa, V.K., Haken, H., & Kelso, J.A.S. (1996). Extending the HKB model of coordinated movement to oscillators with different eigenfrequencies. *Biological Cybernetics*, *74*, 21–30.
- Haken, H., Kelso, J.A., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics*, *51*, 347–356.
- Kaminski, T.R. (2007). The coupling between upper and lower extremity synergies during whole body reaching. *Gait & Posture*, *26*, 256–262.
- Kawashima, N., Nozaki, D., Abe, M.O., & Nakazawa, K. (2008). Shaping appropriate locomotive motor output through interlimb neural pathway within spinal cord in humans. *Journal of Neurophysiology*, *99*, 2946–2955.
- Kelso, J.A.S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge: MIT Press.
- Kelso, J.A.S., Holt, K.G., Rubin, P., & Kugler, P.N. (1981). Patterns of human interlimb coordination emerge from the properties of non-linear, limit cycle oscillatory processes: theory and data. *Journal of Motor Behavior*, *13*, 226–261.
- Kelso, J.A.S., Southard, D.L., & Goodman, D. (1979). On the nature of human interlimb coordination. *Science*, *203*, 1029–1031.
- Kuhtz-Buschbeck, J.P., Brockmann, K., Gilster, R., Koch, A., & Stolze, H. (2008). Asymmetry of arm-swing not related to handedness. *Gait & Posture*, *27*, 447–454.

- McCrae, D.A., & Rybak, I.A. (2008). Organization of mammalian locomotor rhythm and pattern generation. *Brain Research. Brain Research Reviews*, *57*, 134–146.
- Marks, R. (1997). The effect of restricting arm swing during normal locomotion. *Biomedical Sciences Instrumentation*, *33*, 209–215.
- Schöner, G., & Kelso, J.A.S. (1988). Dynamic pattern generation in behavioral and neural systems. *Science*, *239*, 1513–1520.
- de Sèze, M., Falgairolle, M., Viel, S., Assaiante, C., & Cazalets, J.R. (2008). Sequential activation of axial muscles during different forms of rhythmic behavior in man. *Experimental Brain Research*, *185*, 237–247.
- Swinnen, S.P., Dounskaia, N., Levin, O., & Duysens, J. (2001). Constraints during bimanual coordination: the role of direction in relation to amplitude and force requirements. *Behavioural Brain Research*, *123*, 201–218.
- Swinnen, S.P., Young, D.E., Walter, C.B., & Serrien, D.J. (1991). Control of asymmetrical bimanual movements. *Experimental Brain Research*, *85*, 163–173.
- Umberger, B.R. (2008). Effects of suppressing arm swing on kinematics, kinetics, and energetics of human walking. *Journal of Biomechanics*, *41*, 2575–2580.
- Ustinova, K.I., Feldman, A.G., & Levin, M.F. (2006). Central resetting of neuromuscular steady states may underlie rhythmical arm movements. *Journal of Neurophysiology*, *96*, 1124–1134.
- Walter, C.B., & Swinnen, S.P. (1990). Kinetic attraction during bimanual coordination. *Journal of Motor Behavior*, *22*, 451–473.
- Zehr, E.P., Balter, E.J., Ferris, D.P., Hundza, S.R., Loadman, P.M., & Stoloff, R.H. (2008). Neural regulation of rhythmic arm and leg movement is conserved across human locomotor tasks. *The Journal of Physiology*, *582*, 209–227.