Neuromuscular-Skeletal Origins of Predominant Patterns of Coordination in a Rhythmic Two-Joint Arm Movement

Aymar de Rugy
Stephan Riek
Richard G. Carson
Perception and Motor Systems Laboratory
School of Human Movement Studies
The University of Queensland, Brisbane, Australia

ABSTRACT: The authors tested for predominant patterns of coordination in the combination of rhythmic flexion-extension (FE) and supination–pronation (SP) at the elbow-joint complex. Participants (N = 10) spontaneously established in-phase (supination synchronized with flexion) and antiphase (pronation synchronized with flexion) patterns. In addition, the authors used a motorized robot arm to generate involuntary SP movements with different phase relations with respect to voluntary FE. The involuntarily induced in-phase pattern was accentuated and was more consistent than other patterns. This result provides evidence that the predominance of the in-phase pattern originates in the influence of neuromuscular–skeletal constraints rather than in a preference dictated by perceptual–cognitive factors implicated in voluntary control. Neuromuscular–skeletal constraints involved in the predominance of the in-phase and the antiphase patterns are discussed.

Key words: bifunctional muscle, multijoint coordination, neuromuscular–skeletal constraint, predominant pattern of coordination, rhythmic movement

The existence of predominant patterns of coordination in rhythmic interlimb movements is well established. The best-characterized examples are the in-phase (a relative phase relation of 0° between the limbs) and the antiphase (a relative phase of 180°) patterns, which have been investigated and reported primarily in the context of bimanual coordination (e.g., Cohen, 1971; Kelso, 1984). The origins of these predominant patterns of coordination are the subject of intense debates in the literature, with some investigators emphasizing the role of neuromuscular coupling (e.g., Carson & Kelso, 2004), whereas others are partisans of the perceptual–cognitive factor associated with motor control (e.g., Mechsner, 2004; Mechsner, Kerzel, Knoblich, & Prinz, 2001). In the context of rhythmic multijoint movements, the situation is further complicated by the superimposition of additional neuromuscular–skeletal constraints and by the influence of intersegmental dynamics. The first aspect includes the reflexes that link the activity of different muscles acting at the same limb (e.g., Gielen, Ramaekers, & Zuylen, 1988; Naito, 2004) as well as the influence of biarticular muscles acting simultaneously at different joints (e.g., Prilutsky, 2000; Sergio & Ostry, 1994). The second aspect, intersegmental dynamics, includes the influence of interaction torques, that is, the rotational counterpart of forces developed on a segment because of the motion of other segments attached to it (e.g., Hasan, 1991). In learning a relative phase of 90° between elbow and wrist flexion–extension, Buchanan (2004) showed, for instance, that the majority of the participants spontaneously established a 90° lag (instead of a lead) of the wrist with respect to the elbow in order to exploit interaction torques produced at the wrist as a result of elbow movement.

In the present study, we focused on the neuromuscular–skeletal constraints by using a task that involved rhythmic movement of two orthogonal degrees of freedom (df) of the arm and minimized the influence of interaction torques. We tested for a predominant pattern (or patterns) of coordination during the combination of flexion–extension (FE) and supination–pronation (SP) movements at the elbow-joint complex. In addition to the minimal role of intersegmental dynamics, our choice of movements was also motivated by previous identification of the neuromuscular–skeletal constraints that may originate in a predominant pattern (or patterns) of coordination. The most potent of those is likely to result from the mechanical action of the biceps brachii, a muscle that contributes to both flexion and supination movements (e.g., Ettema, Styles, & Kipers, 1998). Because of its biarticular influence, in particular, the biceps brachii has been the

Correspondence address: Aymar de Rugy, Perception and Motor Systems Laboratory, School of Human Movement Studies, Room 424, Building 26, The University of Queensland, Brisbane, QLD 4072, Australia. E-mail address: aymar@hms.uq.edu.au
subject of a good deal of study in relation to its role in the control of arm movement (e.g., Etema, Taylor, North, & Kippers, 2005; Naito, 2004; Naito et al., 1998; Sergio & Ostry, 1994). In the context of discrete isometric target-acquisition tasks, the modulation of biceps activity has proved to be a crucial element of skill acquisition in tasks combining flexion and supination (Shemmell et al., 2005). Correspondingly, the adaptation of biceps activity was found to be a limiting factor for the learning of combined flexion and pronation by older adults (Barry, Warman, & Carson, 2005). In view of these considerations, we hypothesized that the action of the biceps would favor in-phase synchronization between flexion and supination movements (or, equivalently, between extension and pronation), and expected, therefore, that the in-phase pattern of coordination would be predominant.

To evaluate the involuntary effect of the neuromuscular-skeletal constraints that may promote a predominant pattern (or patterns) of coordination, we designed experimental conditions that involved an involuntary entrainment of one degree of freedom (df) on the other. Those constitute the main body of the study. We sought to differentiate the potential influence of neuromuscular-skeletal constraints from a preference for a pattern of coordination dictated by the perceptual factors implicated in voluntary control (e.g., Mechsner, 2004). To do so, we elicited rhythmic entrainment of SP onto FE at different phase relations by means of torques applied by a motorized robot arm. The frequency (0.77 Hz) and amplitude (90°) of a voluntary rhythmic FE movement were specified, respectively, by a metronome and visual feedback. Simultaneously, torques in different phase relations with respect to FE motion were applied in the SP-df. Although the participants were given no specific instruction with respect to SP movement, we expected the entrainment of SP by FE to be more accentuated and more consistent (i.e., less variable) for the in-phase relation than for the other phase relations.

Materials and Method

Participants

Ten participants (8 men and 2 women, aged 23–36 years) volunteered for this experiment. All were right-handed and had normal or corrected-to-normal vision. Participants were naive to our purpose in the experiment. They all gave their informed consent before the experiment; the experimental protocol was approved by the Medical Research Ethics Committee (The University of Queensland) and conformed to the Declaration of Helsinki.

Apparatus and Materials

Each participant sat in a chair 1 m from a computer display positioned at eye level. With their right hand, participants grasped a handle at the end of a 2-df robot arm that permitted elbow FE and forearm SP (see Figure 1). The center of rotation of the FE and SP movements of the arm coincided with those of the robot arm. The moment arm associated with force resulting from FE movement about the SP axis of rotation was small, and interaction torque at SP-df caused by FE movement was assumed negligible.

Two servo-controlled torque motors (Baldor BSM 4250AA, Fort Smith, AR) applied torques separately in each df of the robot arm. We applied a flexion torque on the FE-df to compensate for the gravitational torque associated with the weight of the apparatus \((T_{GF, FE} = 12.1 \times \cos \theta_{FE})\). Both motors were instrumented with encoders that determined angular position along FE- and SP-df (\(\theta_{FE}\) and \(\theta_{SP}\)). Zero degrees in FE-df corresponded to a horizontal forearm position (elbow at 90°), and 0° in SP-df corresponded to a vertical handle position (forearm midpronation). Flexion and supination were represented as positive angles. We recorded angular position data at a sampling rate of 1000 Hz.

Added stiffness. The motor applied a torque representing a mechanical stiffness \((T_{S, FE}\) and \(T_{S, SP}\)) to each df of the robot arm. We set the stiffness terms so that the resonance frequencies for both FE- and SP-df equaled the frequency imposed in the experiment (0.77 Hz). We achieved that equality with \(k_{FE} = 13\) Nm/rad \((T_{S, FE} = -k_{FE}\theta_{FE})\) and \(k_{SP} = 0.43\) Nm/rad \((T_{S, SP} = -k_{SP}\theta_{SP})\), for FE and SP, respectively. Our rationale for that design is as follows: The displacement of a second-order linear system driven at resonance by a sinusoidal torque typically lags the torque by 90°. Thus, we could infer, for example, that for a movement in flexion synchronized with a movement in supination, the torques in flexion and supination also coincide.

Added torque. In conditions of involuntary SP movement, we applied an added torque in the SP-df as a function of the state of the FE-df. To generate specific relative phase relations between FE and SP motion, we used four different functions. The added torque \(T_{A, SP}\) was, respectively, (a) a positive function of FE position \((K+)\), (b) a negative function of FE position \((K-)\), and (c) a positive \((B+)\) and (d) a negative \((B-)\) function of FE velocity, as follows:

\[
T_{A, SP} = K \theta_{A, SP} + B \theta_{FE}.
\]

FIGURE 1. Experimental setup.
with $K = k_1 > 0$ and $B = 0$ for Condition K+; $K = -k_1$ and $B = 0$ for K−; $K = 0$ and $B = b_1 > 0$ for B+; and $K = 0$ and $B = -b_1$ for B−. Condition B+ promoted an in-phase relation (i.e., a relative phase of 0° [peak flexion coincident with peak supination]) between FE and SP movement. In the definitive case, B+ provides an oscillatory torque $T_{ASP}$ that is a positive function of $\theta_F$, and thus leads $\theta_F$ by 90°. Providing that $T_{ASP}$ is close to a harmonic oscillation, and because the motion occurs at resonance frequency, that torque gives rise to an SP oscillation ($\theta_{SP}$) that lags $\theta_F$ by 90°, thus being in phase with $\theta_F$. Alternatively, B− favors an antiphase relation (i.e., 180° [peak flexion coincident with peak pronation]); That condition provides a torque $T_{ASP}$ that differs from $\theta_F$ by 180°. Conditions K+ and K− favored relative phase relations between FE and SP oscillatory movements of 90° and 270°, respectively. Note that a relative phase of 90° corresponded to FE movements that led SP movements by 90°.

In addition, we used two levels of added torques, T1 and T2. T1 corresponded to the minimum level of torque required to just overcome the inertia and damping (in the SP-df) associated with the robot arm and to generate on its own a small (less than 2°) SP movement. We achieved that with $k_1 = 0.86 \text{ Nm/rad}$ and $b_1 = 0.18 \text{ Nm/rad/s}$. The second level of torque, T2, was sufficient to generate an SP amplitude of approximately 50°. For T2, $k_2 = 1.07 \text{ Nm/rad}$ and $b_2 = 0.22 \text{ Nm/rad/s}$.

Visual feedback. We provided visual feedback only for the FE movement with a horizontal line that moved vertically on the screen and had a displacement proportional to the extent of FE motion. Elbow flexion gave rise to an upward movement of the line on the screen, and elbow extension to a downward movement. A prescribed amplitude of 90° was indicated by two stationary horizontal bars (targets), centered on locations corresponding to 45° flexion and 45° extension.

Procedure and Design

Participants were required to produce an FE oscillation between the two targets at the frequency prescribed by a metronome (0.77 Hz) that provided a beep for each half-cycle of motion. In conditions of involuntary SP movements, we gave no specific instructions to participants with respect to the generation of movement in the SP-df. Each trial started with the first metronome beep and lasted 35 s. Three practice trials were presented before the acquisition sessions. Three experimental blocks were then conducted, each composed of nine trials: one per combination of level and phase of added torque ($2 \times 4 = 8$), to which we added one control trial without additional torque. We added the control trial to test for involuntary SP movement in the absence of additional torque. Within each block, the order of those nine trials was fully randomized. Three trials involving voluntary control of SP movement were conducted without added torque at the end of the experiment. In those trials, we asked the participants to intentionally produce an SP oscillation of their choice in conjunction with the FE oscillation constrained as in the rest of the experiment. We designed those voluntary trials to test for a predominant pattern (or patterns) of coordination between FE and SP movements. The entire experiment lasted 45 min.

Data Reduction and Dependent Measures

We low-pass filtered the time series of the FE and SP angular displacements by using a zero-lag second-order Butterworth filter with a cutoff frequency at 8 Hz. We excluded the first 10 s of each trial from analysis to avoid contamination by transient behavior.

Because the different relative phases promoted in the experimental conditions relied on the assumption that $T_{ASP}$ was close to a harmonic oscillation, we computed the degree of harmonicity $H$ of $T_{ASP}$ as the deviation of the $T_{ASP}$ trajectory from a perfect circle in the phase space—that is, the space spanned by $T_{ASP}$ and its temporal derivative. To that end, we mean-adjusted and normalized $T_{ASP}$ and its temporal derivative. The radius of each sample in the phase space was determined, and $H$ was computed for each trial as the root mean square error between the radial trajectory and a perfect harmonic oscillation with unit radius (e.g., Sternad, Turvey, & Saltzman, 1999). The angular impulse of $T_{ASP}$ for both the pronation and the supination torques were further calculated as the temporal integral of $T_{ASP}$ in those respective directions. For each trial, we averaged the angular impulse $I$ of the pronation and the supination added torque per cycle of FE movement.

Using a peak-picking algorithm, we determined the frequency $f$ (in Hz) and amplitude $A$ (in degrees). We further calculated the standard deviation of the frequency (SDf) and the coefficient of variation of the amplitude (CVA). We identify dependent variables related to FE and SP by using subscripts (e.g., $f_{SP}$ refers to the frequency obtained in the SP-df).

We determined the relative phase between FE and SP oscillatory movements by using circular statistics (Fisher, 1993). To that end, we mean-adjusted the angular position and normalized the angular velocity by dividing the velocity signal by the mean frequency. Phase angles were computed as the arctangent of the angular position and velocity extracted from phase space. The mean circular relative phase $\psi$ was determined as the arctangent of the ratio between the means of the cosine and sine of the difference between the phase angle for FE and SP (for more detail, see, e.g., Russell & Sternad, 2001). In that calculation, FE movement was taken as the reference, meaning that $\psi = 10^\circ$ indicated that FE led SP by 10°. We calculated a measure of dispersion of circular relative phase, uniformity $U$, according to Fisher. Because that measure is bounded by 0 and 1 and is nonlinear with respect to the distribution around the mean relative phase angle, we converted it into a measure of dispersion SD$\psi$ that varies approximately linearly between 0 and infinity according to the following:

$$SD\psi = (−2\log U)^{1/2}.$$ 

High values of SD$\psi$ denote high variability.
Statistical Analyses

We averaged dependent variables related to FE per participant and experimental condition, and analyzed them by using two-way 2 (level of torque: T1 and T2) × 4 (condition of added torque) repeated measure analyses of variance (ANOVAs). We conducted a similar ANOVA on harmonicity $H$ and performed a three-way 2 (direction: pronation vs. supination) × 2 (level of torque) × 4 (condition of added torque) repeated measures ANOVA on impulse $I$. Dependent variables related to SP and to the relative phase between FE and SP were similarly averaged and were analyzed separately for the two levels of torque. We designed the latter analysis to focus the statistical power of the inferential tests because we expected very different behaviors for each level of torque. Because we also hypothesized that behavior in Condition B+ (which was expected to induce an in-phase pattern of coordination) would be different from those in the other conditions, we conducted planned comparisons between Condition B+ and Conditions K+, B−, and K−. The significance level was set to $p < .05$. We report the proportion of total variability attributable to the concerned factor as values of partial eta-squared ($\eta^2$; see Pierce, Block, & Aguinis, 2004, for information about partial $\eta^2$ measures).

Results

FE Oscillatory Movement

None of the two-way repeated measures ANOVAs relating to $f_{FE}$, $SDf_{FE}$, $A_{FE}$, and the $CVA_{FE}$ revealed significant effects; $p$s > .15 and $\eta^2$s < .17 for all statistical tests. FE oscillatory movement was thus not affected by the level and the phase of the interaction torque. The overall averages for $f_{FE}$ ($SDf_{FE}$) and $A_{FE}$ ($CVA_{FE}$) were, respectively, 0.773 Hz (0.011 Hz) and 90.06° (3.18°). Those outcomes confirm that participants reliably produced the frequency and amplitude imposed by the task.

Reliability of the Motor Torque Developed in the Different Experimental Conditions

The two-way repeated measures ANOVA on $H$ revealed an effect of the experimental condition only, $F(3, 7) = 16.51, p = .001, \eta^2 = .88$; $T_{SP}$ was less harmonic for Conditions B+ ($H = .050$) and B− ($H = .051$) than for Conditions K+ ($H = .033$) and K− ($H = .032$). Despite those differences, the values of $H$ were small, and $T_{SP}$ proved to deviate only slightly from a perfect harmonic oscillation, as illustrated by the trajectory of $T_{SP}$ plotted for two representative trials in Figure 2.

The three-way repeated measures ANOVA on $I$ revealed an effect of the level of torque, $F(1, 9) = 2128.8, p = .000, \eta^2 = .99$. The averaged angular impulses per cycle were 0.065 Nms and 0.081 Nms for T1 and T2, respectively. Apart from that effect, the averaged impulse per cycle could not be differentiated between the directions (pronation vs. supination) and between the experimental conditions.

SP Oscillatory Movement

On average, $f_{SP}$ (0.774 Hz) was close to the frequency imposed by the metronome, and no effects of phase of added torque on $f_{SP}$ were observed for T1, $p = .238, \eta^2 = .433$, and for T2, $p = .427, \eta^2 = .311$.

The planned comparison on $SDf_{SP}$ obtained for T1 revealed Condition B+ (0.047 Hz) to be less variable than Condition K+ (0.072 Hz), $F(1, 9) = 43.82, p = .000, \eta^2 = .830$, but not different from Conditions B−, $p = .324, \eta^2 = .108$, and K−, $p = .526, \eta^2 = .046$. For T2, $SDf_{SP}$ was less variable for Condition B+ (0.017 Hz) than for Condition K− (0.030 Hz), $F(1, 9) = 13.12, p = .006, \eta^2 = .593$, but not different from Conditions K+, $p = .066, \eta^2 = .327$, and B−, $p =

![Figure 2](image-url)
.266, \( \eta^2 = .135 \). SD/\( \delta \) for T1 (0.057 Hz) was approximately double that of T2 (0.025 Hz), as can be seen in Figure 3A.

The planned comparisons on movement amplitude \( \text{ASP} \) obtained for T1 did not reveal any significant effects, \( p > .12 \) and \( \eta^2 < .215 \) for all comparisons. For T2, however, \( \text{ASP} \) was greater in Condition B+ than in Condition K+, \( F(1, 9) = 15.58, p = .003, \eta^2 = .634 \), and in Condition K−, \( F(1, 9) = 8.35, p = .018, \eta^2 = .481 \), but did not differ from that in Condition B−, \( p = .203, \eta^2 = .173 \). As shown in Figure 3B, ASP was greater in B+ (54.46°) than in K+ (29.17°), B− (40.56°), and K− (26.54°). The overall averaged amplitude of the SP oscillation was smaller for T1 (7.58°) than for T2 (37.69°).

The only difference revealed by planned comparison on CVA/\( \text{ASP} \) concerned the second level of torque (T2), in which \( \text{CVA/ASP} \) obtained for B+ (17.48%) was found to be significantly lower than that obtained for K− (27.52%), \( F(1, 9) = 11.17, p = .009, \eta^2 = .554 \). For all other planned comparisons, there were no reliable effects, \( p > .078, \eta^2 < .306 \). As can be seen in Figure 3C, CVA/\( \text{ASP} \) for T1 (50.6%) was approximately double that for T2 (24.7%) and was systematically smaller for Condition B+ than for the three other interaction torque conditions.

**Relative Phase and Its Variability**

Significant effects of phase of added torque were obtained on \( \psi \) for both T1, \( F(3, 27) = 663.4, p = .000, \eta^2 = .987 \), and T2, \( F(3, 27) = 2760.8, p = .000, \eta^2 = .999 \). As can be observed in Figure 3D, \( \psi \) was found to be close to the patterns of relative phase favored by the sole influence of interaction torque (see Method section). That is, \( \psi \) was close to in-phase for Condition B+ (\( \psi = -22.2° \) and -4.7° for T1 and T2, respectively); close to antiphase for B− (\( \psi = 160.0° \) and 176.4° for T1 and T2, respectively); and close to 90° (\( \psi = 62.6° \) and 75.1° for T1 and T2, respectively) and 270° (\( \psi = 252.9° \) and 259.5° for T1 and T2, respectively) for K+ and K−, respectively.

For T2, SD/\( \psi \) was smaller in Condition B+ than in Conditions K+, \( F(1, 9) = 6.78, p = .029, \eta^2 = .430 \), and K−, \( F(1, 9) = 12.60, p = .006, \eta^2 = .583 \), but did not differ from Condition B−, \( p = .180, \eta^2 = .191 \). Figure 3E depicts the smaller SD/\( \psi \) obtained for T2 in B+ (0.17) than in K+ (0.32), B− (0.26), and K− (0.31). For all planned comparisons for T1, there were no reliable effects, \( p > .133, \eta^2 < .232 \). The overall averaged SD/\( \psi \) obtained for T1 (0.63) was approximately twice that obtained for T2 (0.27).

**Control Trials Without Added Torque**

The peak-picking algorithm used was unable to identify a reliable frequency of movement for the SP-\( \delta \) for trials without interaction torque, and the SP amplitude never exceeded 1°. We conclude that no SP oscillation was obtained on those trials.

**Voluntary Trials**

SP oscillations ranging from 15° to 125° were obtained in the voluntary trials that we conducted at the end of the experiment to test for a predominant pattern (or patterns) of coordination. As illustrated in Figure 4, participants spontaneously established either an in-phase or an antiphase pattern of coordination on almost the totality of the trials. The in-phase pattern (0° ± 15°) was established on 77% of the trials, whereas the antiphase pattern (180° ± 15°) was performed on 20% of trials.

**Discussion**

In accordance with our hypothesis related to the influence of the biceps brachii, which acts both as a flexor and a supinator at the elbow-joint complex, the in-phase pattern in which supination and flexion are synchronized was a clear, predominant pattern of coordination between voluntary SP and FE movements (in-phase pattern was observed on 77% of the voluntary trials). In addition to the in-phase pattern, however, participants spontaneously chose the antiphase pattern in a notable proportion of the voluntary trials (20%). The antiphase pattern, in which pronation is synchronized with flexion, thus appears to be a predominant pattern of coordination, although to less extent than the in-phase pattern. Those results suggest that neuromuscular-skeletal constraints in addition to the biarticular influence of the biceps also contribute to the adoption of specific patterns of coordination.

Turning now to the trials in which involuntary SP movement was induced at different phase relations with respect to the voluntary FE movement, our results confirmed that participants reliably produced the frequency and amplitude imposed by the task with respect to FE movements. Despite the neuromuscular-skeletal constraints that potentially linked the motion of those 2 d/f/s, no influence of the involuntary SP movement on the voluntary FE was found for the different induced phase relations. The analysis of the profiles of torques induced in SP as a function of FE movements further confirmed that that torque was close to a harmonic oscillation and provided the same impulse in both pronation and supination, irrespective of the phase relations that were induced. Apart from an influence of the neuromuscular-skeletal constraints, whose effects would depend on the phase induced, there is thus no reason for the involuntary SP movement to differ between the different conditions of a given level of torque. On the other hand, the relative phase relations induced by the experimental conditions were close to those intended.

The results obtained on SP when the lower level of torque was applied did not reveal a clear effect of the different conditions of induced phase relationships. The only reliable difference concerned the variability of the SP frequency, which was lower for Condition B+ than for Condition K−. The overall variability of the motion generated when that lower level of torque was applied was, however, substantially higher than it was for the higher level of torque. The results obtained when the higher level of torque was applied were more compelling. The amplitude of SP was substantially higher for the in-phase-induced phase relation (Condition B+) than for the other patterns of entrainment. The in-phase
FIGURE 3. Dependent variables plotted as a function of the experimental conditions (B+, K+, B−, and K−) for the two levels of torque (T1 and T2). (A) Standard deviation of supination–pronation oscillation frequency, SDfSP. (B) Supination–pronation amplitude, ASp. (C) Coefficient of variation of ASp, CVASp. (D) Mean circular relative phase ψ. (E) SDψ. According to the experimental design, conditions B+, K+, B−, and K− were supposed to induce phase relationships between FE and SP movements of 0°, 90°, 180°, and 270°, respectively. Error bars represent 95% confidence intervals.
moment arm about the FE axis is less than half that of the biceps brachii, the action of the pronator teres is likely to favor an antiphase pattern in which elbow flexion is synchronized with pronation. The synergistic activity of other muscles (e.g., brachioradialis, triceps brachii, and pronator teres, alone or in combination) in conjunction with biceps brachii, which has the effect of compensating for undesired bifunctional actions of that muscle during selective flexion or supination, or during the combination of flexion with pronation or extension with supination, has been reported numerous times (e.g., Cnockaert, Lensel, & Pertuzon, 1975; Ettema et al., 2005; Jamison & Caldwell, 1993; Sergio & Ostry, 1994, 1995; Zuylen, Gielen, & Denier van der Gon, 1988). In circumstances in which synergistic activity compensates adequately for the bifunctional actions of biceps brachii, a context may thus be provided for the expression of the bifunctional role of pronator teres and for the generation of an antiphase pattern of coordination across the two mechanical dfs.

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