Chapter 5

Discrete execution of continuous unimanual rhythmic wrist movements: additive effects of musculoskeletal and informational constraints

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Abstract

Rhythmic movements, which are continuous by definition, are often geared toward particular discrete points in the movement cycle, so-called anchor points, which have been postulated to reflect task-specific information and/or musculoskeletal properties that may aid rhythmic movement production. The present experiment was conducted to gain insight into the relative contribution of informational (metronome beats) and musculoskeletal (wrist postures) mediators of anchoring by systematically varying those mediators over movement reversal points. In particular, participants cycled their right wrist in a flexed, neutral, or extended posture, either self-paced or synchronized to the beat of a metronome pacing peak flexion, peak extension, or both peak flexion and extension. The effects of those manipulations were assessed in terms of kinematics, auditory-motor coordination, and muscle activity. Anchoring phenomena depended on the compatibility of musculoskeletal and informational factors, which had largely independent effects. This independence was evidenced further by concomitant systematic changes in muscular activity that were directly associable with anchoring. The quality and parsimony of task execution appeared to depend on the observed number and precise location of the anchor points in the movement cycle: while more anchor points seemed to enhance accuracy, less anchor points seemed to be more economical.
Continuous rhythmic limb movements, such as wrist oscillations, typically exhibit near sinusoidal to-and-fro trajectories. However, the execution of continuous movements may take a discrete form when movements are consistently oriented at a particular point in the movement cycle (Chapters 2-4; Beek, 1989; Byblow et al., 1994; Carson et al., 1994; Fink et al., 2000; Ivry et al., 2002; Maslovat et al., 2006; Pressing 1998, 1999; Repp 2005; Wachholder & Altenburger, 1926; Zelaznik et al., 2005). In his study of juggling, Beek (1989) submitted that rhythmic movements are often organized around certain spatial locations serving as intentional attractors or organizing centers within and for the limit cycle. That is, by timing the movement to particular points in the movement cycle, the cyclical activity as a whole is timed. In such cases, movement trajectories are consistently oriented toward discrete points in the movement cycle as evidenced by a reduced local variability of the limit cycle trajectories. Such points of reduced trajectory variability are called anchor points (Chapters 2-4; Beek, 1989; Byblow et al., 1994; Carson et al., 1994; Fink et al., 2000; Maslovat et al., 2006).

On the one hand, anchor points may reflect points or regions in the perceptual-motor workspace where task-specific information is available (Beek, 1989), such as information about the required timing when rhythmic limb movements are coordinated in synchrony with an external pacing signal. On the other hand, anchor points may also reflect points or regions in the perceptual-motor workspace where functional, task-related neuromuscular properties are exploited (Chapter 3), such as the possibility to store and release energy (Guiard, 1993). These musculoskeletal or mechanical properties may be utilized by actively orienting or anchoring movements to those points. Indeed, for rhythmic wrist oscillations with the wrist joint in extreme positions only activation of shortened agonist muscles is observed, suggesting that the rebound is substantiated by passive moments of elongated antagonist muscles (e.g., Esposti et al., 2005; Wachholder & Altenburger, 1926; see also Carson et al. (2000) for related findings pertaining to pronation-supination rotations).

In line with these possible origins of anchoring, Maslovat et al. (2006) distinguished between informational and mechanical anchor points. However,
the assumption underlying this terminology is that a given anchor point (i.e., point of reduced variability in the movement cycle) either reflects informational or mechanical constraints on movement execution, while both constraints may in fact be operative at the same point. An interesting observation in this context was made by Byblow and colleagues (1994), who demonstrated that in self-paced rhythmic forearm rotations points of maximal pronation were characterized by lower endpoint variability than points of maximal supination, allegedly related to inherent neuromuscular differences between contributing muscle groups. They further showed that the performance of acoustically paced bimanual in- and antiphase rhythmic movements was most stable when maximal pronation rather than maximal supination was time-locked with the pacing signal. The in-phase supination-on-the-beat pattern and the two antiphase patterns often switched to in-phase pronation-on-the-beat with increasing metronome frequencies (see also Carson et al., 2000), that is, the pattern of coordination in which metronome beats synchronized with the anchor point location identified in unpaced forearm rotations. This example illustrates how, in the terminology of Maslovat et al. (2006), informational and mechanical constraints of anchoring may coincide at a single point in the movement cycle. This raises the need to experimentally determine the relative contribution of informational and mechanical constraints to the discrete execution of continuous rhythmic movements.

Although both acoustic pacing (Byblow et al., 1994; Fink et al., 2000; Kelso et al., 1990) and wrist posture (Chapters 2 and 3) are known to evoke anchor points, their combined effect has not been studied in a systematic and well-controlled manner. The present experiment seeks to fill this lacuna so as to gain insight into the processes underlying the discrete, i.e., anchoring-based, execution of continuous rhythmic movements. To this end, participants were invited to oscillate their hand with the wrist in a flexed, neutral, or extended posture, either unpaced or paced by an acoustic metronome in a flex-on-the-beat, extend-on-the-beat, or flex-and-extend-on-the-beat pattern. By positioning the wrist in either a flexed or extended posture, a mechanical mediator of anchoring was induced at peak flexion or extension, respectively (M in Table 5.1). Likewise, the pacing signal provided an informational mediator of anchoring at peak flexion and extension in flex-on-the-beat and extend-on-the-beat conditions, respectively (I in Table 5.1). The informational constraints are...
Chapter 5

101

Table 5.1

| Schematic overview of experimental conditions and experimentally induced single mechanical or informational (M and I) mediators of anchoring. Lower case letters are used if those constraints are balanced over endpoints. |
|---|---|---|---|---|
| no pacing flex-on-beat extend-on-beat double pacing | flexion | extension | flexion | extension |
| M | M | M | M |
| flexed | I | I | i | i |
| m | m | m | m | m | m | m | m |
| neutral | I | I | i | i |
| M | M | M | M |
| flexed | I | I | i | i |
| m | m | m | m |

Specific expectations for each of these conditions may be derived from the general assumption that informational and mechanical mediators of anchoring are independent of each other and that hence their effects are additive (e.g., Chapter 3; Byblow et al., 1994). We therefore expected anchoring on peak flexion (extension) when M and I here coincide, that is for the flex(extend)-on-the-beat condition with the wrist flexed (extended). In the double pacing condition with the wrist flexed (extended), we expected a bias to anchoring on peak flexion (extension) resulting in reduced peak excursion variability and shorter movement duration in the anchored direction (cf. Chapter 3), because here the induced mechanical mediators of anchoring (M) are added to balanced informational mediators (i).

By the same logic, we expected anchoring on peak flexion in the flex-on-the-beat condition and on peak extension in the extend-on-the-beat condition with the wrist in a neutral posture (I added to balanced m).

Although no specific expectations followed from the assumption of independence for the conditions in which informational and mechanical anchor points were opposing (e.g., flex-on-the-beat with the wrist extended or extend-on-the-beat with the wrist flexed; M and I at opposite endpoints) or in balance (neutral posture with no pacing or double pacing), those conditions were crucial in determining the relative contribution of informational and mechanical constraints on the discrete execution of continuous rhythmic movements.

Contents under embargo
In addition to the conventional analyses of anchor points in terms of kinematic measures, we also assessed muscular activity underlying these anchoring phenomena to identify possible muscle-specific differences in their instantiation. This is an important complementary analysis because, to the best of our knowledge, studies on anchoring have thus far been limited to the level of kinematics. This is unfortunate because there are indications to expect systematic changes in muscle activity when rhythmic wrist movements are timed to a specific point in the movement cycle (e.g., Esposti et al., 2005; Wachholder & Altenburger, 1926). In particular, Wachholder and Altenburger (1926) already noted that when subjects placed a voluntary emphasis on either the flexion or extension phase during rhythmic finger, hand, or forearm cycling (so-called "Betonung"); pp. 630-631), movements in the accentuated direction lasted shorter and frequently began with a discontinuity at or near the unaccentuated reversal point. These kinematic signs of "Betonung" were accompanied by changes in flexor and extensor muscular activity: a longer period of stronger activity was observed in the accentuated direction, followed by a relatively long "Pause" prior to the onset of muscular activity corresponding to the unaccentuated direction (p. 632 and Figure 6 on p. 635). These early observations suggest that accentuating or emphasizing movements at a particular point in the movement cycle, which is reminiscent of the notion of anchoring, are brought about by changes in the duration, timing, and amplitude of muscular activity. Following the pioneering work of Wachholder and Altenburger (1926), we expected that the muscle(s) instantiating movement in the anchored direction would show increased activity and longer burst duration, as well as modifications in the relative timing between flexor and extensor bursts.

**Methods**

**Participants**

Thirteen subjects (six males, seven females, aged 19-29 years) volunteered to participate in the study. All were right-handed according to their scores on a shortened version of the Edinburgh handedness inventory (mean laterality quotient: 79.0%; Oldfield 1971). Participants gave their written informed consent prior to the experiment, which was approved by the local ethics committee before it was conducted.

*Contents under embargo*
Apparatus
Participants were seated in a height-adjustable chair with their right forearm resting on a tabletop with adjustable supports to prevent forearm movement and to secure its neutral position (i.e., centered between pronation and supination extremes). Only flexion and extension movements about the wrist were allowed. The right hand was strapped against a flat vertically-oriented manipulandum (fingers extended and thumb up) mounted on a potentiometer whose axis was aligned with the wrist’s flexion-extension axis. Surface electromyograms (EMG) were obtained from m. flexor carpi radialis (FCR) and m. extensor carpi radialis (ECR). After cleansing and abrasion of the skin, disposable electrodes were positioned in the center of the muscle belly on the line from origin to insertion in a bipolar arrangement with a center-to-center distance of two centimeters. Computer-produced acoustic pacing signals (custom-made digital metronome, consisting of 50-ms beeps with a frequency of 440 Hz) were presented through a speaker positioned in front of the participants. Wrist angular position, EMG signals and acoustic pacing signals were synchronously sampled at 1000 Hz. During stationary wrist posture and practice trials (see below), a semicircular projection bow was positioned at a distance of about 2 m at 2 o’clock in front of the participant providing concurrent visual feedback of wrist angular position. The projection bow consisted of a continuous array of 448 light-emitting diodes (LEDs) representing wrist angular position over a range of 150°. During experimental trials online feedback was visible for the experimenter only as the LED bow was rotated towards the experimenter and participants were instructed to direct their gaze at a smiley positioned at eye-height two meters in front of them (at 12 o’clock). A cover prevented vision of the moving hand.

Procedure
Prior to the experiment proper, participants were instructed to perform smooth oscillatory movements about the right wrist in time with a 3 Hz metronome in such a way that peak flexion and peak extension both coincided with a beep. Only participants that were able to stably perform this double pacing condition within three practice trials were included in the experiment (one candidate participant failed to meet this criterion). After these selection trials the EMG electrodes were applied. The remaining 12 participants then performed

Contents under embargo
Chapter 5

104

maximum voluntary contractions (MVC) by generating twice a maximal isometric flexion or extension torque about the right wrist for approximately 3 s. The experiment examined wrist cycling in three wrist postures (i.e., flexed, neutral, and extended) crossed with four acoustic pacing conditions (i.e., no pacing, flex-on-the-beat, extend-on-the-beat, double pacing), resulting in 12 experimental conditions. Participants performed all conditions six times, for a total of 72 trials per participant. Trials were presented in blocks with the three wrist postures providing the first level of blocking (3 × 24 trials) and acoustic pacing (4 × 6 trials) the next. The first trial was always a practice trial in which participants received concurrent visual feedback of their wrist angular position and movement amplitude. In the next five trials, the LED bow was rotated towards the experimenter and participants were instructed to direct their gaze to the smiley in front of them to prevent potential gaze anchoring effects (cf. Chapters 3 and 4; Neggers & Bekkering, 2001). The order of the wrist posture blocks was counterbalanced over the 12 participants (with each order being performed by two participants). The acoustic pacing blocks within the wrist posture blocks were presented in (semi-)random order with the restriction that the experiment never started with the no pacing condition (see below).

At the start of each wrist posture block, participants were positioned comfortably in the apparatus and the range of motion of the wrist was determined. Specifically, participants were invited to adopt a maximal flexion and extension position, each for about 5 s. The center in between flexion and extension extremes was taken as the neutral position. Subsequently, participants performed a series of nine stationary wrist angular position trials to estimate the necessary muscular effort for maintaining these positions against the forces generated by joint stiffness. The following wrist angular positions were examined in random order: -60°, -45°, -30°, -15°, 0°, 15°, 30°, 45°, and 60°. Note that 0° corresponded to the individual neutral wrist angular position (i.e., corrected for offset) and that the range of experimental wrist postures fell well within the individually determined maximal range of motion (155.0°±13.5°). Participants were instructed to maintain the LED signal within a tolerance of ±2.5° from the designated position (as indicated by a marker) for 10 s during which wrist angular position and EMG signals were recorded.

Then one of the three wrist posture blocks was performed. Specifically, participants performed wrist oscillations of 15° amplitude (range 30°) around -45°, 0°, and 45° in flexed, neutral, or extended blocks, respectively.
were instructed to cycle their hand as smoothly as possible and to synchronize peak flexion (extension) to the beat of the metronome in the flex(on-the)-beat condition. In these single pacing conditions the metronome frequency was 1.5 Hz, whereas in the double pacing condition the metronome frequency was 3.0 Hz. In the latter condition, flexion and extension excursions had to be synchronized to consecutive beats, so that the resulting movement frequency was also 1.5 Hz. In the no pacing condition, participants were instructed to cycle their hand as smoothly as possible at about the same rate as the acoustically paced trials. All trials lasted 30 s (i.e., 45 cycles for pacing trials). To facilitate trial initiation, the experimenter guided the hand to the flexion excursion position in the flex-on-the-beat condition (i.e., -60°, -15°, and 30° for flexed, neutral, and extended wrist posture blocks, respectively) and to the extension excursion position in the extend-on-the-beat condition (i.e., -30°, 15°, and 60° for flexed, neutral, and extended wrist posture blocks, respectively). In the no pacing and double pacing conditions, the hand was guided to the required center region (i.e., -45°, 0°, or 45°). Trials were repeated if the mean amplitude range deviated more than 10° from the required range, if mean wrist posture during the trial deviated more than 10° from the prescribed mean wrist posture (i.e., -45°, 0°, or 45°), or if mean movement frequency deviated more than 0.01 Hz from the prescribed frequency in the pacing trials (leading to drift in the phase relation between hand excursions and metronome beats) while for the no pacing condition mean movement frequencies lower than 1.4 Hz or higher than 1.6 Hz were penalized. Each wrist posture block lasted approximately 25 minutes after which a break of at least 5 minutes was introduced. The experiment lasted 2 to 2.5 hours in total, including breaks.

Data analysis MVC and stationary trials

FCR and ECR recordings were first band-pass filtered (10-400 Hz, second-order bi-directional Butterworth filter) and subsequently whitened using a fifth-order autoregressive filter (Staude & Wolf, 1999). The highest root mean square (RMS) value in 250 ms windows in the two MVC attempts was defined as the MVC value and used for normalization. For each static position trial, the average RMS value (normalized to MVC) over the last 7 s was used to obtain a measure for the muscular effort to maintain that specific position.
Data analysis experimental trials

Preprocessing and trial selection. We had to exclude 11 trials from further analysis due to data collection errors. Potentiometer data (hand movement) of the remaining trials were low-pass filtered using a second-order bi-directional Butterworth filter (cut-off frequency: 15 Hz). The first five cycles of each trial were excluded to eliminate possible transient effects. To ensure that movement frequencies were comparable between paced and unpaced conditions, we excluded 16 trials in the no pacing condition using the criterion $1.40 > f > 1.60$ Hz. To evaluate whether task requirements were met for acoustic pacing trials, coupling of hand excursions to metronome beats was determined. Specifically, the phase $\psi$ (in °) was quantified relative to the metronome for each cycle as $\psi_i = 360° \cdot (t_{y,i} - t_{x,i})/(t_{x,i+1} - t_{x,i})$, where $t_{y,i}$ indicates the time of the $i$th peak flexion (extension) excursion and $t_{x,i}$ corresponds to the moment of the $i$th metronome beat that specified peak flexion (extension) excursion (cf. Ridderikhoff et al., 2005). A positive value of $\psi$ implies that the hand ($y$) was lagging the metronome beat ($x$). For each trial, a segment of 20 cycles was selected showing 1:1 frequency synchronization (i.e., no drift in $\psi$) with the required phase relation between hand excursions and metronome beats, identified using the following criteria: a) mean movement frequency $f$ (defined as the inverse of the mean period between consecutive maximal wrist extensions) between 1.49 and 1.51 Hz, b) mean $\psi$ between -90° and 90°, and c) standard deviation of $\psi$ less than 27°. Circular statistics (Mardia, 1972) was used to calculate the mean and standard deviation of $\psi$ over segments. These criteria were violated in 13 acoustic pacing trials, which were excluded from further analysis. For the remaining 680 trials (94.4% of the total data set), several dependent variables were calculated quantifying task performance, local and global kinematics, and EMG.

Task performance. Task performance was evaluated in terms of mean movement frequency $f$, mean amplitude $A_\theta$ of wrist angular position time series $\theta$, and the deviation from the required mean wrist position $\Delta \theta_{req}$ (defined as the difference between the required center of oscillation and the center in between mean flexion and extension movement reversal points; negative (positive) $\Delta \theta_{req}$ indicated that the wrist was on average more flexed (extended) than required).
Local and global kinematics. We determined the spatial variability of maximal wrist flexion and extension excursions by calculating the respective standard deviations ($\sigma_{\text{spatial}}$ in °). Furthermore, we quantified flexion and extension peak-to-peak temporal variability ($\sigma_{\text{temporal}}$ in ms). Apart from these two local kinematic characteristics, global properties of the wrist oscillations were assessed by means of phase portraits (i.e., wrist angular velocity $\theta$ as a function of wrist angular position $\theta$) and Hooke's portraits (i.e., wrist angular acceleration $\theta$ as a function of $\theta$). To this end, $\theta$ was mean centered and normalized to unit amplitude (i.e., -1 and +1 imply mean peak flexion and mean peak extension excursions, respectively). The movement duration of flexion and extension half cycles was taken based on time instances of peak flexion and peak extension and normalized to % cycle duration. Next, $\theta$ was computed from $\theta$ and normalized to $2\pi f$. Likewise, $\theta$ was computed from $\theta$ and again normalized to $2\pi f$. Hooke's portraits were constructed separately for flexion and extension half cycles, which were cut from normalized $\theta$ and $\theta$ time series using time indices of peak flexion and extension. After time-normalization to 100 points per half cycle using a spline interpolation procedure, average $\theta$ and $\theta$ time series for flexion and extension half cycles were computed for each trial of each participant. A harmonic oscillator is represented by a straight line in a Hooke's portrait (i.e., $\theta = -\theta$) and the amount of variance that can be attributed to a harmonic oscillation can be readily quantified by the $r^2$ of the linear regression of $\theta$ onto $\theta$ (i.e., $r^2 = 1$ for a purely harmonic oscillation). The explained variance of anharmonicities was expressed as $NL = 1 - r^2$ (Chapter 3; Mottet & Bootsma, 1999; for a similar approach see Beek & Beek, 1988).

Auditory-motor coordination. For the acoustic pacing trials, auditory-motor coordination was defined in terms of $\psi$ by calculating the mean and standard deviation of $\psi$ for each trial (i.e., $\psi$ and $\sigma_{\psi}$, respectively) using circular statistics (Mardia, 1972). To compare $\psi$ and $\sigma_{\psi}$ between flexion and extension excursion points, $\psi$ of unpaced reversal points for single metronome conditions was determined relative to the midpoint between consecutive beats (cf. Balasubramaniam et al., 2004).

EMG. FCR and ECR recordings were first band-pass filtered and whitened (see analysis for MVC and stationary trials). To visualize the average muscle activity...
within a movement cycle, 16 bins were defined in relation to the phase of the hand movement ($\Theta$), defined by $\tan(\Theta) = \theta/2\pi f$. Thus, each bin represented an equal part of the phase of the hand oscillation. The first and ninth bin were centered around $\Theta = 0°$ (peak flexion) and $\Theta = 180°$ (peak extension), respectively. For each bin the RMS value of the EMG was calculated and normalized to MVC.

In addition, a more fine-grained analysis of the bursting behavior of the muscles was performed. To this end, the method of Staude and Wolf (1999) was adopted that uses an approximate generalized likelihood test to detect local changes in the statistical properties of the EMG (so-called change times) using sliding test windows $W$ of 40 samples and a conservative decision threshold ($h = 20$; Staude & Wolf, 1999). RMS values of the EMG between successive change times were calculated to objectively determine which intervals corresponded to bursts. To this end, we first selected the tentative ‘OFF’ intervals with RMS values lower than the median. Subsequently, bursts (and the corresponding onsets and offsets) were identified as those intervals for which the RMS value of EMG activity exceeded the mean plus twice the standard deviation of the EMG activity in these tentative ‘OFF’ intervals. For quantitative analysis of bursting behavior, we determined the number of bursts, the duration of bursts (% cycle duration), normalized EMG activity during a burst (the ‘ON’ amplitude: $A_{ON}$) and normalized EMG activity between bursts (the ‘OFF’ amplitude: $A_{OFF}$). Finally, to analyze the timing of these bursts, the relative phasing of onsets and offsets with respect to the phase of the movement ($\Theta_{onsets}$ and $\Theta_{offsets}$, respectively) was determined, with 0° indicating that the onsets/offsets coincided with peak flexion (for ECR) or peak extension (for FCR).

Statistical analysis

Means of all dependent variables were calculated per included trial and subsequently averaged per condition for each participant. For all participants, means were based on at least three valid trials per condition. To determine the effects of acoustic pacing and wrist posture, dependent variables of task performance, local and global kinematics, and auditory-motor coordination were submitted to a repeated measures analysis of variance (ANOVA) with within-subject factors direction (2 levels: flexion, extension; for $f$, $A_{\theta}$, $\Delta \theta_{req}$, and $NL$). Contents under embargo
Chapter 5

Contents under embargo
A θ of 15°. For f, a significant Wrist Posture × Pacing Condition interaction was observed (F(2.07,22.75) = 5.79, p = 0.009, 2pη = 0.345), indicating that in unpaced wrist cycling f was significantly greater for neutral (1.53 Hz) than flexed (1.50 Hz) or extended (1.49 Hz) wrist postures. In acoustic pacing trials, no differences between postures were observed; f was on average 1.50 Hz with a very small standard deviation (0.002 Hz). For Δθ req, a near significant effect of wrist posture (flexed: 0.87°, neutral: 0.23°, extended: -0.99°; F(2,22) = 3.38, p = 0.052, 2pη = 0.235) was observed, suggesting that in extreme wrist positions the center of oscillation deviated towards a more neutral posture. A significant effect of acoustic pacing was observed (F(2.46,27.08) = 5.73, p = 0.006, 2pη = 0.342); post hoc analyses indicated a shift in center of oscillation towards flexion and extension in flex-on-the-beat (-1.69°) and extend-on-the-beat (1.08°) conditions, respectively.

Figure 5.1. Average EMG for FCR (gray) and ECR (black) muscles as a function of a series of static wrist positions θ. Negative θ values: flexed wrist posture; positive values: extended wrist postures; 0°: individually determined neutral posture. Error bars represent standard error.

Local kinematics. A significant Direction × Posture interaction was found for σspatial (F(2,22) = 42.6, p < 0.001, 2pη = 0.795); flexion σspatial increased significantly from flexed (1.57°) to neutral (2.06°) to extended (2.55°) postures.
Figure 5.2. Three-way interaction of A) spatial endpoint variability (σ_{spatial}) and B) movement duration, presented for all experimental conditions. Flexed, neutral, and extended wrist postures are represented by dark, intermediate, and bright gray bars.

Flexion and extension σ_{spatial} or movement duration are indicated by solid and hatched bars, respectively. Asterisks indicate significant differences between both sides within a condition (p < 0.05). Error bars represent standard error. Mechanical and informational mediators of anchoring are indicated as in Table 5.1.

and vice versa for extension σ_{spatial} (2.31°, 2.11°, and 1.92°, respectively), resulting in significantly lower σ_{spatial} at the reversal point corresponding to the posture manipulation compared to the other reversal point. In a neutral posture no difference in σ_{spatial} was observed between the two reversal points.

Contents under embargo
Furthermore, a significant Direction × Posture × Pacing interaction was observed ($F(6,66) = 3.1, p = 0.010, \eta^2 = 0.220$; see Figure 5.2A). Post hoc comparisons between flexion and extension $\sigma_{\text{spatial}}$ within each condition indicated that flexion ($\sigma_{\text{spatial}}$) was always lower than extension ($\sigma_{\text{spatial}}$) with flexed (extended) postures, which was in line with abovementioned Direction × Posture interaction. In the neutral posture, flexion $\sigma_{\text{spatial}}$ was smaller than extension $\sigma_{\text{spatial}}$ for flex-on-the-beat or double-pacing conditions, suggesting anchoring on peak flexion in these conditions, whereas without acoustic pacing and in the extend-on-the-beat condition no significant differences in endpoint variability were observed (Figure 5.2A).

For $\sigma_{\text{temporal}}$ significant effects of posture, pacing, and Direction × Posture were observed ($F(2,22) = 21.0, p < 0.001, \eta^2 = 0.657, F(3,33) = 17.8, p < 0.001, \eta^2 = 0.617,$ and $F(1.24,13.63) = 7.80, p < 0.011, \eta^2 = 0.415,$ respectively). Post hoc analyses showed that overall $\sigma_{\text{temporal}}$ was larger with the wrist extended (37.2 ms) than for neutral (26.8 ms) and flexed (28.2 ms) wrist postures. Furthermore, overall $\sigma_{\text{temporal}}$ decreased significantly from unpaced (34.2 ms) via single pacing (31.2 ms and 31.5 ms for flex-on-the-beat and extend-on-the-beat conditions, respectively) to double pacing (26.2 ms) conditions. The interaction entailed that flexion $\sigma_{\text{temporal}}$ was smaller than extension $\sigma_{\text{temporal}}$ for cycling with a flexed posture (25.5 ms vs. 30.8 ms) and vice versa for an extended posture (40.7 ms vs. 33.8 ms). No difference was observed in the neutral posture (27.0 ms vs. 26.7 ms).

Global kinematics. A significant Direction × Posture interaction ($F(2,22) = 15.0, p < 0.001, \eta^2 = 0.577$) was found for movement duration. Flexion phase duration was significantly shorter than extension phase duration for cycling with the wrist flexed (48.31% vs. 51.69%) and vice versa for cycling with the wrist extended (51.27% vs. 48.73%). Flexion and extension duration did not differ for wrist cycling in a neutral posture (49.81% vs. 50.19%). In addition, significant Direction × Pacing and Direction × Posture × Pacing interactions were observed for movement duration ($F(3,33) = 17.4, p < 0.001, \eta^2 = 0.613$ and $F(6,66) = 2.8, p = 0.017, \eta^2 = 0.203,$ respectively). The two-way interaction entailed that flexion lasted shorter than extension in flex-on-the-beat conditions (47.8% vs. 52.2%) and vice versa for extend-on-the-beat conditions (51.2% vs. 48.8%); the difference in movement duration was more pronounced for flex-on-the-beat than...
extend-on-the-beat conditions (4.4% vs. 2.4%). Flexion and extension durations did not differ from each other in the unpaced (50.2% vs. 49.8%) and double pacing (50.0% vs. 50.0%) conditions. The three-way interaction indicated that the greater difference in movement duration in the flex-on-the-beat condition was due to the extended wrist posture in which flexion duration (47.8%) did not differ from that in neutral (48.7%) and flexed (46.8%) postures (see also Figure 5.2B), indicating an attempt to anchor on peak flexion with the wrist extended when flexion was paced.

Figure 5.3. Hooke's portraits, averaged over participants, as a function of acoustic pacing (columns) and wrist posture (rows) conditions with flexion and extension half cycles indicated in gray and black, respectively. Mechanical and informational anchoring constraints are indicated as in Table 5.1.

The most striking aspect of the averaged Hooke's portraits of flexion (gray) and extension (black) half cycles for each combination of wrist posture and acoustic pacing presented in Figure 5.3 was the systematic deviation from $\theta = -\theta$ (representing harmonic oscillation with low NL) with extreme wrist positions. A significant effect of posture ($F(2,22) = 16.7, p < 0.001, \eta^2 = 0.602$) was observed for NL. Whereas for the neutral posture wrist cycling was quite ...
sinusoidal (NL = 0.072), it was significantly less harmonic for flexed (NL = 0.099) and extended (NL = 0.138) postures. Moreover, NL was significantly larger for extended than flexed postures, a finding that may be related to the overall increased $\sigma_{\text{temporal}}$ for extended wrist postures. No effects of acoustic pacing on NL were observed. Note, however, that NL just represents a scalar to quantify deviations from harmonicity, irrespective of the precise nature of these anharmonicities. As can be seen in Figure 5.3 (bottom panels), the characteristic profile for the extended posture was reversed when beats specified peak flexion, a finding in line with the three-way interaction of movement duration.

Auditory-motor coordination. For acoustic pacing trials local adjustments of hand excursions to metronome beats were further assessed using $\psi$ and $\sigma_{\psi}$. Like Esposti et al. (2007) and Ridderikhoff et al. (2005) we observed that hand movements were on average slightly lagging metronome beats ($\psi = 27.8° \pm 5.2°$). Furthermore, significant Direction × Posture ($F_{(2,22)} = 9.76, p < 0.001, \eta^2 = 0.470$), Direction × Pacing ($F_{(2,22)} = 33.2, p < 0.001, \eta^2 = 0.751$) and Direction × Posture × Pacing ($F_{(4,44)} = 3.78, p = 0.010, \eta^2 = 0.256$) interactions were observed for $\psi$. These effects basically indicated that $\psi$ was smaller in anchored directions. Specifically, post hoc analyses indicated that flexion $\psi$ was smaller than extension $\psi$ (21.9° vs. 28.2°) with a flexed posture and vice versa for an extended posture (29.6° vs. 26.5°); in the neutral posture $\psi$ did not differ between sides (30.6° vs. 29.9°). Likewise, in the flex-on-the-beat condition flexion $\psi$ was smaller than extension $\psi$ (19.4° vs. 26.3°) and vice versa for the extend-on-the-beat condition (30.7° vs. 26.2°); in the double pacing condition $\psi$ did not differ between sides (32.0° vs. 32.0°). The three-way interaction was caused by differences between conditions of conflicting mechanical and informational anchoring constraints, that is, flexion $\psi$ did not differ in the extend-on-the-beat condition with the wrist flexed (25.2° vs. 26.9°), whereas in the flex-on-the-beat condition with the wrist extended flexion $\psi$ was smaller than extension $\psi$ (24.2° vs. 32.3°).

For $\sigma_{\psi}$ significant effects of posture ($F_{(2,22)} = 13.3, p < 0.001, \eta^2 = 0.547$), pacing ($F_{(2,22)} = 23.2, p < 0.001, \eta^2 = 0.679$), and Direction × Posture interaction ($F_{(1.23,13.47)} = 6.46, p = 0.020, \eta^2 = 0.370$) were observed. Like $\sigma_{\text{temporal}}, \sigma_{\psi}$ was significantly larger with the wrist extended (15.4°) than with flexed (13.6°) or neutral (12.6°) wrist postures. The effect of pacing revealed
that \( \sigma \psi \) was smaller with double (12.0°) than with single pacing (14.7° and 14.9° for flex- and extend-on-the-beat conditions, respectively). In addition, flexion \( \sigma \psi \) was smaller than extension \( \sigma \psi \) with the wrist flexed (13.1° vs. 14.2°) and vice versa for the extended posture (16.5° vs. 14.3°); in the neutral posture no difference in \( \sigma \psi \) was observed (12.6° vs. 12.6°).

**Figure 5.4.** Effects of flexed, neutral, and extended wrist postures on phase portraits (upper panels) and muscle activity (lower panels). Upper panels: typical phase portraits as obtained for unpaced wrist cycling in the three postures for a single participant. The black circle indicates a harmonic oscillation. Lower panels: for each wrist posture, normalized EMG amplitudes for FCR (gray) and ECR (black) muscles, determined for 16 phases of the movement cycle, were averaged over participants and acoustic pacing conditions; error bars represent the corresponding standard error.

EMG. In the static wrist position trials we observed systematic increments in EMG amplitudes of ECR in extended positions and FCR in flexed positions (Figure 5.1). The presence of a notable passive joint torque also had profound effects on the EMG patterns during rhythmical wrist cycling. Figure 5.4 clearly shows the typical reciprocal FCR-ECR activation pattern for wrist cycling in a neutral posture (Esposti et al., 2005; Riddetikhoff et al., 2005). As can be seen, contents under embargo
ECR and FCR were less engaged in flexed and extended postures, respectively, indicating that corresponding extension and flexion torques were generated passively. Representative phase portraits for these unpaced conditions are presented, summarizing abovementioned effects of posture on excursion variability (i.e., systematic variations in the locations of local thinning of the phase portrait), movement duration (i.e., asymmetries in peak velocity), and harmonicity (i.e., greater deviation from harmonic oscillation, represented by the dark circle), for flexed and extended postures.

The active contribution of each muscle was quantified in terms of the average number of EMG bursts per trial. The significant Muscle × Posture interaction \( F(2,22) = 56.4, p < 0.001, \eta^2 = 0.837 \) underscored the general pattern shown in Figure 5.4: a smaller number of FCR bursts in the extended (9.8) than in neutral (18.4) or flexed (22.3) postures, whereas for ECR the opposite pattern was observed with less bursts in flexed (9.3) than neutral (16.7) and extended (19.9) postures. In view of the small number of bursts in flexed and extended positions for ECR and FCR, respectively, further analysis of EMG bursts only included flexed and neutral positions for FCR and extended and neutral positions for ECR to preclude potentially unreliable estimates of mean burst duration and mean on- and offset phasing due to inconsistent timing of a small number of bursts only. Furthermore, EMG measures for included conditions were not determined if the number of detected FCR or ECR bursts was less than 10. This led to missing values for 3 participants. The following EMG results are therefore based on the remaining 9 participants and on neutral and extreme wrist posture conditions, allowing for comparison of bursting behavior of FCR in the flexed position to that of ECR in the extended position.

In addition to the global bursting pattern (Figure 5.4) and the number of bursts, mechanical differences between neutral and extreme postures also had systematic effects on EMG amplitudes (A_ON and A_OFF), the burst duration, and on- and offset timing (\( \Theta_{onsets} \) and \( \Theta_{offsets} \); statistics are summarized in Table 5.2). It is noteworthy that from these measures, only burst duration and on- and offset timing (\( \Theta_{onsets} \) and \( \Theta_{offsets} \)) were also affected by acoustic pacing (Table 5.2).

Finally, the absence of significant three-way interactions in EMG activity implies that the position-induced mechanical effects on EMG measures were generally independent from the acoustic pacing effects. In the following, EMG results are described separately for wrist posture and acoustic pacing effects.

Contents under embargo
Table 5.2

<table>
<thead>
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<th>Effect</th>
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<th>p</th>
<th>η²</th>
<th>F</th>
<th>p</th>
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<td>21.0</td>
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<td>0.684</td>
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<td>&lt;0.001</td>
<td>0.800</td>
<td>31.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pacing</td>
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<td>0.221</td>
<td>0.165</td>
<td>1.1</td>
<td>0.360</td>
</tr>
<tr>
<td>Muscle × Pacing</td>
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<td>&lt;0.001</td>
<td>0.373</td>
<td>4.0</td>
<td>0.058</td>
</tr>
<tr>
<td>Posture × Pacing</td>
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<td>0.663</td>
<td>0.003</td>
<td>0.5</td>
<td>0.770</td>
</tr>
<tr>
<td>Muscle × Posture × Pacing</td>
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<td>0.183</td>
<td>0.180</td>
<td>0.4</td>
<td>0.753</td>
</tr>
</tbody>
</table>

Effects of wrist posture on EMG measures. Mean burst duration demonstrated significant effects of muscle and posture and the Muscle × Posture interaction. Bursts were shorter for FCR (31.0%) than for ECR (49.4%) and longer for extreme (43.5%) than neutral (36.9%) postures. The interaction entailed that FCR bursts were longer in extreme (37.1%) than in neutral (24.9%) positions in the absence of a posture-mediated difference for ECR (i.e., 49.9% vs. 48.9%).

For both Θ onsets and Θ offsets a significant effect of muscle was observed (Table 5.2). As could be expected, onsets of FCR (-10.5°, just before peak extension) and ECR (-26.3°, just before peak flexion) were approximately a half-cycle apart, with significantly later onsets for FCR. We further observed earlier FCR offsets (111.2°, just after peak flexion) than ECR offsets (157.1°, just before maximal extension). The difference in Θ onsets and Θ offsets between muscles accounted for identified differences in burst duration.

Contents under embargo
addition, for Θ offsets a significant effect of posture was observed, showing later offsets in extreme than in neutral postures (156.6° and 111.8°), probably to overcome increased counteracting passive torque. Finally, a significant Muscle × Posture interaction was observed for Θ onsets; post hoc analyses indicated earlier onsets for ECR in neutral (-44.6°) than in extreme (-8.1°) positions but, in contrast, earlier onsets for FCR in extreme (-19.3°) than in neutral (-1.7°) postures.

The significant posture effect and Muscle × Posture interaction for A ON indicated that A ON was higher in extreme (8.2%) than neutral (5.9%) positions and that this amplitude difference was larger for ECR (9.7% vs. 5.9%) than for FCR (6.6% vs. 5.8%). For A OFF significant muscle, posture, and Muscle × Posture interaction effects were observed (Table 5.2). A OFF was higher for ECR (2.4%) than for FCR (1.4%) and higher in the extreme (2.2%) than in the neutral posture (1.6%). The interaction indicated that both main effects were due to larger AOFF for ECR in extreme (3.0%) than neutral (1.7%) postures, as post hoc analyses revealed no other significant differences (AOFF FCR: 1.4% vs. 1.4%).

Effects of acoustic pacing on EMG measures. For burst duration a significant Muscle × Pacing interaction was observed, indicating that ECR bursts lasted relatively shorter (44.3%) in the extend-on-the-beat condition than in other pacing conditions (unpaced: 48.5%, flex-on-the-beat: 53.7%, double pacing: 51.1%). In contrast, FCR bursts lasted relatively longer in the extend-on-the-beat condition (34.3%) than in unpaced (29.5%), flex-on-the-beat (29.4%), and double pacing (30.8%) conditions. For Θ onsets a near significant Muscle × Pacing interaction was observed (p = 0.058), which might suggest that shorter burst durations in anchored directions were (in part) due to later onsets of corresponding EMG activity (FCR; unpaced: -9.1°, flex-on-the-beat: -7.0°, extend-on-the-beat: -19.0°, double pacing: -7.0°, and ECR; unpaced: -30.4°, flex-on-the-beat: -35.7°, extend-on-the-beat: -14.9°, double pacing: -24.4°). This suggestion was underscored further by the fact that Θ offsets was affected significantly by pacing and the Muscle × Pacing interaction. FCR offsets occurred earlier in pacing conditions for which a shorter burst duration was observed (unpaced: 100.5°, flex-on-the-beat: 106.9°, double pacing: 110.8°) than for the extend-on-the-beat condition (Θ offsets = 126.6°). Likewise, Θ offsets for ECR occurred somewhat earlier in the extend-on-the-beat condition (152.6°).
Chapter 5

Discussion

The present study examined the discrete execution of continuous rhythmic movements by systematically manipulating mechanical and informational mediators of anchoring (see Table 5.1). The assumption that those mediators were independent, and hence produced additive effects, was corroborated empirically. Marked anchoring effects were observed in conditions where balanced informational or mechanical anchoring constraints were complemented by induced single mechanical or informational mediators of anchoring ($M$ or $I$), respectively. Furthermore, conditions where $M$ and $I$ stood in conflict were instrumental in delineating the relative contribution of mechanical and informational constraints on task execution. Ambiguous kinematic results for these two conditions were resolved by complementary findings of muscular activity, uncovering neuromuscular signatures of anchoring and differences therein between flexor and extensor muscles. Below we discuss these findings and their theoretical and practical implications in more detail.

Mechanical mediator of anchoring

As expected, wrist cycling with flexed and extended wrist postures mediated anchoring at peak flexion and peak extension, respectively, as evidenced by reduced spatial and temporal variability at the anchored endpoint, shorter movement duration in the anchored direction and decreased overall harmonicity (Figures 5.2-5.4). It has been suggested that at these anchor points task-specific mechanical or neuromuscular properties are exploited to organize the cyclical act, such as the possibility to store and release energy (Chapter 3; Guiard, 1993). EMG results provided firm support for this interpretation by identifying counteracting passive moments in static (Figure 5.1) and dynamic (Figure 5.4) situations. As can be seen, the amount of muscular activity scales with deviations from neutral static wrist positions. Furthermore, the typical phase-dependent reciprocal bursting activity that is characteristic for rhythmic wrist cycling in a neutral posture (e.g., Esposito et al., 2005, Ridderikhoff et al., 2005, Wachholder & Altenburger, 1926) disappeared in extreme wrist postures; ECR (FCR) was predominantly active in wrist cycling with extended (flexed) posture (Figure 5.4).

Contents under embargo
We further observed marked differences between flexor and extensor muscles in terms of burst duration (FCR burst lasted shorter), timing (FCR onsets were later, offsets earlier), and amplitude (FCR amplitude was lower), which, in all likelihood, are related to neuromuscular differences between flexors and extensors (e.g., Bawa et al., 2000; Carson & Kelso, 2004; Carson et al., 2007; Cheney et al., 1991; Delp et al., 1996; Ettema et al., 1998; Gonzalez et al., 1997; Vallbo & Wessberg, 1993). Increased ECR amplitudes during and in between bursts may have accounted for the reduced harmonicity of wrist oscillations in extended postures (Figure 5.3). Furthermore, and more interestingly, the observed significant Muscle × Posture interaction for nearly all EMG measures (Table 5.2) revealed distinct adaptations of FCR and ECR to changes in wrist posture. Higher amplitudes and longer burst durations were to be expected in extreme positions to compensate for increased counteracting passive moments. However, our findings were more subtle in that ECR modulated merely its activity level, whereas FCR modulated its duration and timing. The ability to utilize variations in timing, burst duration, and muscular activity during and in between bursts may be critically important for achieving dexterity, efficiency, and flexibility in motor control. Apparently, flexor muscles are better suited for this purpose than extensor muscles (Bawa et al., 2000; Cheney et al., 1991; Gonzalez et al., 1997, see also below) because extensor muscles less economically had to increase their activity level to adapt to changes in wrist posture.

Informational mediator of anchoring
As is evident from Figure 5.2, single metronome conditions mediated differential anchoring phenomena in expected directions: in the flex-on-the-beat condition, lower flexion than extension spatial endpoint variability was observed and vice versa for the extend-on-the-beat condition. In addition, we observed shorter movement durations and smaller deviations in relative phase $\psi$ between hand excursions and metronome beats in the anchored directions. These effects were evident for cycling with the wrist in a neutral posture and in an extreme posture if induced mechanical and informational mediators of anchoring ($M$ and $I$) coincided. Similar effects were observed for double pacing conditions with the wrist flexed (extended), resulting in anchoring on peak flexion (extension). For all these conditions, the three measures progressed in similar directions.
lending credibility for the assumption that they reflect local ($\sigma$) and global ($\psi$) aspects of anchoring (Chapter 3). Notably, the three-way interactions that were observed for these markers were all associated with flex-on-the-beat with extended wrist and extend-on-the-beat with flexed wrist conditions. Specifically, in the former condition extension spatial endpoint variability was lower, suggesting anchoring at peak extension, while, in contrast, flexion movement duration was shorter and flexion $\psi$ was smaller, suggesting anchoring at peak flexion. The strength of the induced informational mediator of anchoring at peak flexion was underscored further by the fact that the Hooke's portraits for this condition differed qualitatively from those observed in other pacing conditions with the wrist extended (Figure 5.3). Such opposite effects were not observed for the extend-on-the-beat condition with the wrist flexed: flexion endpoint variability was lower, suggesting anchoring on peak flexion, whereas movement duration and $\psi$ did not differ between flexion and extension. These results could be taken to imply that participants' attempts to anchor peak extension to the beat with the wrist flexed were less successful than attempts to anchor peak flexion to the beat with the wrist extended. This may be attributed to the previously alluded to superior dexterity of flexor muscles over extensor muscles. Congruent with this interpretation, we further observed a bias towards anchoring on peak flexion in the double pacing condition with a neutral posture, albeit only in terms of reduced spatial endpoint variability (Figure 5.2A).

Interestingly, changes in muscle EMG with informational mediators on anchoring differed from those observed with mechanical constraints: bursts were generally shorter in anchored directions accompanied by somewhat delayed onsets and earlier offsets of muscular activity. These findings are not fully consistent with the observation of Wachholder and Altenburger (1926), which appears to have been based on a contamination of the qualitatively different EMG effects with the mechanical and informational constraints observed in the present study. Specifically, the longer pause between offsets of accentuated and onsets of unaccentuated movement phases resembled our EMG findings regarding informational mediators of anchoring whereas longer periods of increased muscular activity were congruent with our EMG findings regarding mechanical mediators of anchoring (i.e., FCR showed longer bursts while ECR showed increased AON). The fact that additive effects of both types of anchoring...
constraints were observed for both kinematic and EMG measures strongly supported the assumption that processes underlying informational and mechanical anchoring are independent (Chapter 3).

Theoretical and practical implications of the notion of anchoring

As expected, we found that continuous rhythmic movements were consistently oriented at one particular reversal point when only mechanical mediators of anchoring were present (i.e., unpaced conditions in extreme postures) or when induced mechanical and informational mediators of anchoring coincided (i.e., flex-on-the-beat in flexed posture and extend-on-the-beat in extended posture).

Differential anchoring phenomena were also observed when balanced informational anchoring constraints were added to a single mechanical mediator of anchoring (i.e., double pacing in extreme postures). These findings were underscored by concomitant one-sided EMG activity. In the neutral posture, EMG activity was always reciprocal, indicating that flexor and extensor muscles were active alternately. Nevertheless, also in the neutral posture systematic differences in kinematics and EMG were observed with acoustic pacing, indicating the presence of a single control or anchor point in the movement cycle. That is, in flex-on-the-beat and extend-on-the-beat conditions, kinematic signs of anchoring to peak flexion and peak extension were observed (Figure 5.2), accompanied by subtle, but significant changes in burst duration and timing. Even when informational anchoring constraints were balanced over endpoints in the neutral posture, inducing two control points in the movement cycle, signs of anchoring at peak flexion were observed (Figure 5.2). Apparently, controlling a single point in the movement cycle is more parsimonious than controlling two points in the movement cycle.

For the two conditions where $M$ and $I$ were in conflict anchoring processes were based on two incongruent control points (i.e., at peak flexion and extension). In the flex-on-the-beat condition with the wrist extended indeed clear signs for anchoring on both endpoints were observed (Figures 5.2 and 5.3). In contrast, in the extend-on-the-beat condition with the wrist flexed movements seemed to be oriented predominantly at peak flexion as no clear anchoring phenomena at peak extension were found, presumably because extensor muscles were not as dexterous as flexor muscles. Participants indicated (subjectively) that these two conditions were difficult to perform, suggesting that they were attentionally more demanding. Indeed, using a reaction time task, Carson et al. [2000] found that participants were able to perform the task more accurately when the control point was at peak extension than at peak flexion.

Contents under embargo
Chapter 5

(1999) found that extend-on-the-beat coordination was more attention demanding than flex-on-the-beat coordination. The greater attentional demands required for extending on the beat may thus have prompted participants to anchor on peak flexion in the extend-on-the-beat condition with the wrist flexed. The lower attentional burden associated with flexing in synchrony with a metronome (Carson et al., 1999) may have resulted in the double anchoring strategy in the flex-on-the-beat condition with the wrist extended, so as to comply with task instructions, but possibly at a greater attentional cost (viz. two versus one control point).

Recently, Cabaj and colleagues (2008) provided strong support for increased attentional demands in controlling two versus one point in the movement cycle in a study of rhythmic forearm rotations in time with a metronome pacing either peak pronation or peak supination. The mechanical context was changed by placing the axis of rotation either below or above the long axis of the forearm, inducing activity of pronator or supinator muscle groups, respectively (cf. Carson et al., 2000). Thus, translated to the findings of the present study, in the pronate-on-the-beat condition informational and mechanical mediators of anchoring coincided for the lower rotation axis (i.e., single anchor point) and were in conflict for the upper rotation axis (i.e., two anchor points) and vice versa for the supinate-on-the-beat condition. Greater attentional demands, quantified by pedal response time following visual probe stimuli, were observed for conditions in which mechanical and informational mediators of anchoring were in conflict (Cabaj et al., 2008). In other studies, transitions from conflicting to coinciding mediators of anchoring were observed (e.g., from supinate-on-the-beat to pronate-on-the-beat with the axis below) with increasing movement rates (Byblow et al., 1994; Carson et al., 2000; for a related finding in tapping see the outlier participant of Kelso et al., 1990), supporting the claims that phase transitions in unidirectionally coupled movements have an informational basis (Beek, 1989; Kugler, 1986; Wimmers et al., 1992) and that they are due to thresholds in the associated information processing demands (Rosenbaum, 1991). The synthesis reported above illustrates that these claims can now be condensed empirically into the statement that informational processing demands associated with controlling two points in the movement cycle are relieved when they coalesce to a single control point. Similar transitions from two to one control points could be distilled from the EMG data. We found phase-dependent bursting activity of both ECR and

Contents under embargo
FCR muscles in the neutral posture whereas in extreme postures only one-sided muscular activity was present (Figure 5.4), suggesting active neuromuscular control of two versus one half cycle, respectively. Interestingly, the center of oscillation has been found to shift towards a more extreme position with increasing movement rate (see e.g., Figure 2.8). As a consequence, only one half cycle needs to be controlled while counteracting passive moments (Figure 5.1) bringing the hand out again. In such situations, gradual shifts may be expected from reciprocal to one-sided bursting. Because the center of oscillation constrains passive and active neuromuscular contributions (and thus EMG activity), it is essential to take this aspect into account when studying the neuromuscular characteristics or underpinnings of rhythmic movements. This recommendation is underscored by the small but systematic shifts in oscillation center towards anchored directions with acoustic pacing, which may have assisted participants to also exploit mechanical neuromuscular properties to some degree.

Previous studies reported more stable bimanual in-phase (Kudo et al., 2006) and antiphase (Fink et al., 2000) coordination under double than single metronome conditions. These findings were attributed to a stronger environmental coupling of movement with the double metronome (Fink et al., 2000; Kudo et al., 2006) 8. Although subjective reports suggest that coordinating movements to a double metronome is more difficult, especially at high frequencies (probably related to increased attentional costs associated with controlling two points in the movement cycle), we also found stronger auditory-motor coupling under double than single metronome conditions, as evidenced by overall reduced variability in relative phase (σψ). These findings illustrate that the number and precise location of anchor points may be (co)determined by prevailing cost functions related to task performance (more anchor points may be beneficial) and task economy or computational burden (less anchor points may be more economical).

8 Stabilizing effects of external stimuli are of special interest to rehabilitation programs aimed at improving pathological motor functioning. Gait training after stroke, for example, benefits from rhythmic acoustic stimuli, demonstrating improved walking velocity, gait efficiency, and gait symmetry (e.g., Prassas et al., 1997; Thaut et al., 2007). To optimally implement external cues in rehabilitation programs it is important to know how such informational constraints interact with inherent constraints (e.g., neuromusculoskeletal, intentional) to form the resultant desired movement execution. This knowledge is scarcely available.

Contents under embargo