Human Movement Science 32 (2013) 147–156

Contents lists available at SciVerse ScienceDirect

Human Movement Science

journal homepage: www.elsevier.com/locate/humov

Dimensionality in rhythmic bimanual coordination

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ARTICLE INFO

Article history:
Available online 8 December 2012

PsycINFO classification:
2330

Keywords:
Bimanual coordination
Degrees of freedom
Dynamics
Performance

ABSTRACT

Newell and Vaillancourt (2001) hypothesized that the dimensionality of motor behavior is a function of the level of task performance and the task dynamic. The present study examined high (in-phase), moderate (antiphase) and low (45°, 90°, and 135° relative phase) levels of task performance in bimanual coordination. Estimates of dimensionality were calculated for the component (effector movements), coupling of components (coupling of effectors), and task output (the produced relative phase) levels of analysis. The in-phase coordination mode had lower Approximate Entropy within, and lower Cross-Approximate Entropy between, effector movements than all other modes. The in-phase mode had higher relative phase Approximate Entropy than all other modes. These findings indicate lower effector and coupling dimensionality, and higher relative phase dimensionality, in the in-phase mode. These results support the hypothesis that at the levels of analysis with limit-cycle dynamics high levels of task performance are characterized by lower dimensionality than lower levels of performance. The results also support the hypothesis that high task performance of the fixed-point task goal of maintaining a constant relative phase is characterized by higher dimensionality than low level performance. Together, these findings support and generalize the Newell and Vaillancourt hypothesis to the component, coupling, and task output levels of analysis.

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http://dx.doi.org/10.1016/j.humov.2012.11.003

1. Introduction

A central issue in the control of human movement is how the neuromotor system regulates the numerous degrees of freedom that exist at various biomechanical levels of analysis, such as the skeletal, muscular and neural. This is known as the *degrees-of-freedom problem*. It has been hypothesized that the nervous system addresses this problem by reducing the number of actively regulated (dynamical) degrees of freedom when organizing movements. The dimension of the movement system attractor dynamic is used to capture the number of actively controlled degrees of freedom. A reduction in dimensionality of the motor system has been hypothesized to occur through the constraint of biomechanical degrees of freedom by control structures termed *synergies* or *coordinative structures* (Bernstein, 1967, 1996; Kelso, 1995; Kugler, Kelso, & Turvey, 1980, 1982; Latash, Scholz, & Schöner, 2007; Turvey, 1977, 2007).

Prior research on motor system dimensionality has examined oscillatory finger (Kay, 1988) and hand (Mitra, Amazeen, & Turvey, 1998) movements, pedalo-locomotion (Haken, 1996), posture (Newell, van Emmerik, Lee, & Sprague, 1993), finger tremor (Morrison & Newell, 1996), and tracking tasks (Ganz, Ehrenstein, & Cavonius, 1996).

Research on motor behavior dimensionality has oftentimes been consistent with Bernstein's hypothesis that movements that best meet the task demands are organized by fewer dynamical degrees of freedom than are movements that do not meet the task demands to a high level. For example, Mitra et al. (1998) found lower dimensionality in movements of the right hand (in right handed participants) than of the left during oscillatory bimanual coordination.

However, Newell and Vaillancourt (2001) hypothesized that the association between the level of task performance and the dimensionality of motor output is a function of the task dynamic. In this hypothesis, better performance of motor tasks governed by fixed-point dynamics is organized by control structures of higher dimensionality (i.e., higher dynamical degrees of freedom) than are poor task performances. In movement tasks governed by limit-cycle dynamics the reverse association occurs (i.e., high levels of task criterion performance are associated with low control structure dimensionality).

Experimental evidence has supported the hypothesis of Newell and Vaillancourt that the direction of change in the dimension of the attractor dynamic can increase or decrease depending on the dimension of the task dynamic (Newell, Broderick, Deutsch, & Slifkin, 2003; Newell & Vaillancourt, 2001). Lower levels of error from a constant target goal (i.e., a fixed-point task dynamic) have been associated with higher dimensional output (Newell et al., 2003; Pressing & Jolley-Rogers, 1997; Slifkin & Newell, 1999), while lower levels of error in an oscillatory task (i.e., a limit-cycle task dynamic) have been associated with lower dimensional output (Newell et al., 2003). However, prior research has not simultaneously examined the component, the coupling of components, and the task output levels of analysis.

1.1. Levels of analysis

Possible levels of analysis in motor behavior include the components involved in a task, the coupling of the components, and the task criterion. In bimanual coordination these levels consist of the movements of effectors (the component level), the coupling between effectors (the coupling level), and the maintenance of a target relative phase (the task output level). In the task of maintaining a constant phase relation between rhythmically moving effectors both fixed-point and limit-cycle task dynamics exist on different levels of analysis. The movements of effectors and their coupling are governed by limit-cycle dynamics while the task level of maintaining a constant relative phase value is governed by fixed-point dynamics.

It is possible that the hypothesis of Newell and Vaillancourt (2001) generalizes across the levels of movement analysis (system components, coupling of components, and task output). If this is the case, their hypothesis would predict that the relation between the dimensionality at each level of analysis is a function of the task dynamic and the level of task criterion performance. This possibility has not previously been examined.

Table 1
Representation of the relationship between the levels of analysis, dynamical measures, task dynamic and level of task performance.

Level of Analysis	Task Dynamic	Dynamical Measure	High Level Performance	Low Level Performance
Component (effectors)	Limit-cycle	ApEn	Low	High
Coupling (effector coupling)	Limit-cycle	Cross-ApEn	Low	High
Task Output (relative phase)	Fixed-point	ApEn	High	Low

1.2. Dimensionality and task performance in bimanual coordination

In bimanual coordination the in-phase coordination mode has generally been found to be more stable than the antiphase mode (Kelso, 1984), which is generally more stable than all other bimanual coordination patterns (Zanone & Kelso, 1992). In this way, the highest level of task criterion performance is typically found in the in-phase coordination mode and the lowest level is found in attempts to perform unstable coordination modes (all coordination modes other than in-phase and antiphase). It has also been found that the use of auditory or visual signals, specifying the phase lag between effectors, increases the stability of the in-phase and antiphase, but not unstable, coordination patterns (Fink, Foo, Jirsa, & Kelso, 2000; Maslovat, Lam, Brunke, Chua, & Franks, 2009). In this way, the in-phase and antiphase coordination modes better met the task demands (i.e., lower in task error and variability) with behavioral information than without.

Prior research has found lower dimensionality in the coupling of effectors in high level task performance of the in-phase coordination mode than in lower level task performance of the antiphase mode (James, Molenaar, & Newell, 2011). This is consistent with the lower dimension of poorer task performance in oscillatory movements hypothesized by Newell and Vaillancourt (2001). To date, a study of the dimensionality in bimanual coordination across a range of potential effector phase relations and levels of analysis has not been performed.

The present study estimated dimensionality at different levels of task performance in bimanual coordination. Performance level was operationalized as the in-phase (high level of task criterion performance), antiphase (moderate level of performance), and unstable (low level of performance) coordination modes. Behavioral information was also used to potentially affect the level of task performance. It has previously been shown that the use of auditory behavioral information increases the level of performance (i.e., stability) of the in-phase and antiphase modes (Fink et al., 2000). Analyses were performed at the levels of effector movements, the coupling of effectors and the task level output to estimate the dimensionality associated with high and low levels of task performance in bimanual coordination performance at each level of analysis. Table 1 depicts the relationship between task performance and the levels of analysis examined in the present study.

Newell and Vaillancourt (2001) hypothesized that the direction of change in dimensionality is a function of the dimensionality of the task dynamic. We extended this hypothesis across levels of analysis in a bimanual coordination task. That is, we hypothesized that at levels of analysis in which task performance was oscillatory in nature (the components and the coupling of components) high task criterion performance would be characterized by lower dimensionality than would low task performance. We also hypothesized that high task performance performance of the fixed-point task goal of maintaining a constant relative phase would be characterized by higher dimensionality than would low task performance.

2. Methods

Twenty healthy participants were recruited from the University of Houston student population. All participants identified themselves as right hand dominant and had no hearing deficits as determined by self-report. Participants included 8 males and 12 females between the ages of 20 and 39 (M = 23.6; SD = 4.36) years. All participants provided informed consent as required by the University Institutional Review Board.

2.1. Apparatus

Participants had a custom made cylindrical cardboard sleeve placed over each forearm and hand, grasping a wooden handle inside the distal end of each sleeve. These cylindrical sleeves were of dimension 35 cm (length) × 7.5 cm (diameter), weight 121 grams each and were held in place by two elastic and Velcro straps. Two infrared-emitting diodes were placed on the distal surface of each sleeve, the movements of which were tracked in three dimensions by an Optotrak 3020 (Northern Digital Inc.; Waterloo, Ontario) motion analysis system. As participants' upper arms did not move, two diodes on each cylindrical sleeve captured the relative motion of each sleeve. Kinematic data for each 25 s movement trial were recorded by the Optotrak system at a sampling rate of 200 Hz. A Test Tone Generator auditory metronome with adjustable phase and tone duration settings was used to provide auditory tones. The phase setting on this auditory metronome was set to match trial relative phase conditions.

2.2. Procedures

Participants were seated 3 m in front of, and facing, the Optotrak 3020 system with elbows resting on a padded tabletop and upper arms at approximately a 45° angle. Participant upper arms and elbows were not restrained but subjects were instructed not to change position and were observed to have not moved during performance. Participants were randomly assigned to one of two metronome (continuation and synchronization) groups in which 1.1 Hz auditory tones were provided to control movement frequency and provide behavioral information regarding the phase relation between effectors (Fink et al., 2000; Maslovat et al., 2009; Zanone & Kelso, 1992). Pilot testing indicated this movement frequency was fast enough to cause participants to produce continuous movements rather than to pause at movement endpoints while also remaining slow enough to permit comfortable performance.

Participants assigned to a continuation group heard the auditory metronome for 10 s prior to the collection of data, after which the tones were discontinued and data collection began. Thus, this group had the opportunity to synchronize their movements with the tones but did not have access to this information during data collection. Participants assigned to a synchronization group heard the auditory metronome for 10 s immediately prior to and during data collection. Participants in both groups began flexing and extending their elbows as soon as the metronome began and were requested to synchronize maximal flexion and extension of each arm with the auditory tones. They were instructed to continue these movements, regardless of whether the metronome ceased before or continued during data collection.

The auditory metronome consisted of phase-lagged tones pertaining to each of 5 different relative phase patterns. These were 0° (in-phase), 45°, 90°, 135° and 180° (antiphase). Following the familiarization period participants performed two consecutive 25 s movement trials for each of the relative phase patterns. The 5 relative phase patterns were presented in a random order and 15 s of rest was provided between trials. Participants were instructed not to stop or freeze forearm movements but that adjustments to assist in matching the required coordination pattern could be performed at any time as needed. Participants were blindfolded during the actual performance of all movement trials to prevent the use of visual information.

2.3. Data analyses

Data pertaining to movement of the four infrared light emitting diode markers in the *x*-*y* (sagittal) plane were analyzed to determine the angular position of each forearm at each time point throughout movements. Angular position time-series were filtered with a 4th order recursive 10 Hz lowpass Butterworth filter to eliminate potential equipment noise. The continuous estimate of relative phase (CRP) method was used to determine produced relative phase for each trial (Kelso, 1995). This method consists of normalizing the effector angular position and velocity between 1 and −1 on a cycle-by-cycle basis with relative phase calculated as the right effector phase angle minus the left.

The Rayleigh test was used to determine if relative phase distributions could be distinguished with 95% confidence from a uniform distribution. Any trials determined to not differ significantly from a uniform distribution were to be removed from further analysis. For relative phase time-series that were statistically distinguishable from a uniform distribution the circular mean of relative phase (Batschelet, 1981) was calculated for the 2 trials performed by each participant in each relative phase condition. As the relative phase of bimanual coordination has been shown to differ significantly from a von Mises distribution (the circular equivalent of a Gaussian distribution; James, Layne, & Newell, 2010) information entropy was used to estimate the variability of relative phase. The interpretation of information entropy data does not depend on the assumption that data follow a von Mises (or Gaussian) distribution. Information entropy (Williams, 1997) is calculated as:

$$I_w = -\sum_{i=1}^{N} P_i \log P_i \tag{1}$$

where I_w is information entropy, i is each of a total of N data values and P is the probability of data occurring in each bin. A bin size of 10° was used to determine the probability of relative phase occurrences across the $0° \leftrightarrow 360°$ range.

2.4. Approximate Entropy

Approximate Entropy (ApEn; Pincus, 1991) was calculated to estimate the dimensionality of effector movements and of CRP. ApEn is a low dimensional correlate of estimates of dimensionality such as correlation dimension. Higher ApEn values are indicative of higher dimensionality within time-series. ApEn is calculated as:

$$\mathrm{ApEn}(\vec{X}, m, r) = \log\left[\frac{C_m(r)}{C_{m+1}(r)}\right] \tag{2}$$

where C represents the average recurrence of vectors of length m or $m + 1$ that fall within a range of r in a unit variance normalized time-series, X. Parameter values of $m = 2$ and $r = 0.2$ were used in calculating ApEn as per Pincus (1991).

A common statistical technique known as differencing was used to facilitate stationarity in relative phase time-series so as to allow subsequent analyses within the time domain (Shumway & Stoffer, 2006; Torre & Balasubramaniam, 2011). Differenced CRP data were then analyzed with ApEn to estimate the time-dependent properties of relative phase within trials.

2.5. Cross-Approximate Entropy

The Cross-Approximate Entropy (Pincus & Singer, 1996; Cross-ApEn) between effectors was calculated. This statistic estimates the degree of synchronicity between two signals and is indicative of the dimensionality of control of the two signals (Stergiou, Buzzi, Kurz, & Heidel, 2004). Higher Cross-ApEn values indicate lower time-dependent co-variation and higher dimensionality.

The algorithm for Cross-ApEn is:

$$\mathrm{CrossApEn}(\vec{X}, m, r) = \log\left[\frac{C_m(r)}{C_{m+1}(r)}\right]. \tag{3}$$

This algorithm first counts the C number of m and $m + 1$ pairs of data points across the statistically normalized (mean of zero, variance of 1) time series for the two variables being analyzed (denoted $\vec{X}$), that recur within the range of r. Cross-ApEn is the logarithm of the inverse ratio of the recurrence of $m + 1$ pairs of data points with respect to the recurrence of m pairs of data points. The values of m and r were set at 1 and 0.2, respectively, following the recommendation of Pincus and Singer (1996).

2.6. Inferential statistics

Separate 2 (Group) × 5 (Relative Phase) repeated measures ANOVA were performed for relative phase entropy, the ApEn of effector movements, the Cross-ApEn of effector coupling, and the ApEn of CRP. Analysis of the mean relative phase for each condition was conducted with a Watson-Williams

F-test (the circular equivalent of ANOVA; Batschelet, 1981). Multisample and pairwise comparisons were conducted to determine significant differences across conditions. The calculation of all dependent variables was performed with coded MATLAB (Mathworks, Natick, MA) programs. Inferential statistical analyses were performed using the SPSS software package (version 19.0) with a type-I error of 0.05 used to determine statistical significance. Circular statistical analyses were performed with Oriana (Anglesey, Wales) software. All pairwise comparisons were conducted using the LSD (Least Significant Difference) method.

3. Results

3.1. Mean relative phase

Mean relative phase values for each condition are represented in Fig. 1. The Rayleigh test showed that all trials differed significantly from a uniform distribution. The Watson-Williams *F*-test showed a significant difference existed between relative phase conditions, $F(9190) = 42.50$, $p < .001$. The pairwise comparisons showed that the in-phase CRP was significantly higher in the synchronization group than in the continuation ($p < .001$). The 45°, 90°, 135° and antiphase relative phase did not differ between the two metronome groups.

In the synchronization group the in-phase mode CRP was significantly lower, and the antiphase higher, than all other relative phase conditions (all $p < .001$). CRP in the synchronization 135° condition was significantly higher than in the 45° synchronization group. There were no other significant differences across relative phase conditions in the synchronization group. In the continuation group the in-phase CRP was significantly lower than all other conditions (all $p < .001$). The antiphase CRP was significantly higher than the in-phase ($p < .001$), 90° ($p < .001$), and 135° ($p < .05$), but was not significantly different than the 45° relative phase ($p > .05$). There were no other significant differences across relative phase conditions (all $p > .05$).

3.2. Relative phase entropy

In the ANOVA of relative phase entropy there was no significant main effect for metronome group, $F(1, 18) < 0.001$, $p > .05$. There was a significant main effect for relative phase condition, $F(4, 72) = 40.99$, $p < .001$ (see Fig. 2A). *Post hoc* analysis showed that the in-phase coordination mode was lower than all other modes (all $p < .001$). The antiphase mode was lower than the 90° ($p < .01$) and 135° ($p < .05$) modes but not the 45° ($p > .05$). There were no significant differences between the 45°, 90°, and 135° modes (all $p > .05$). The Relative Phase × Metronome interaction was not significant, $F(4, 72) = 1.08$, $p > .05$.

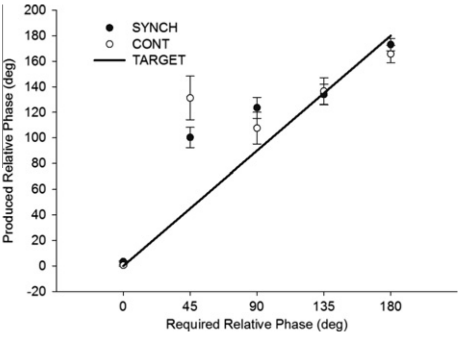

Fig. 1. Data for the mean relative phase are represented as a function of metronome group and required relative phase. SYNCH = Synchronization group; CONT = Continuation group. TARGET = The target relative phase pattern. Standard errors are represented with error bars.

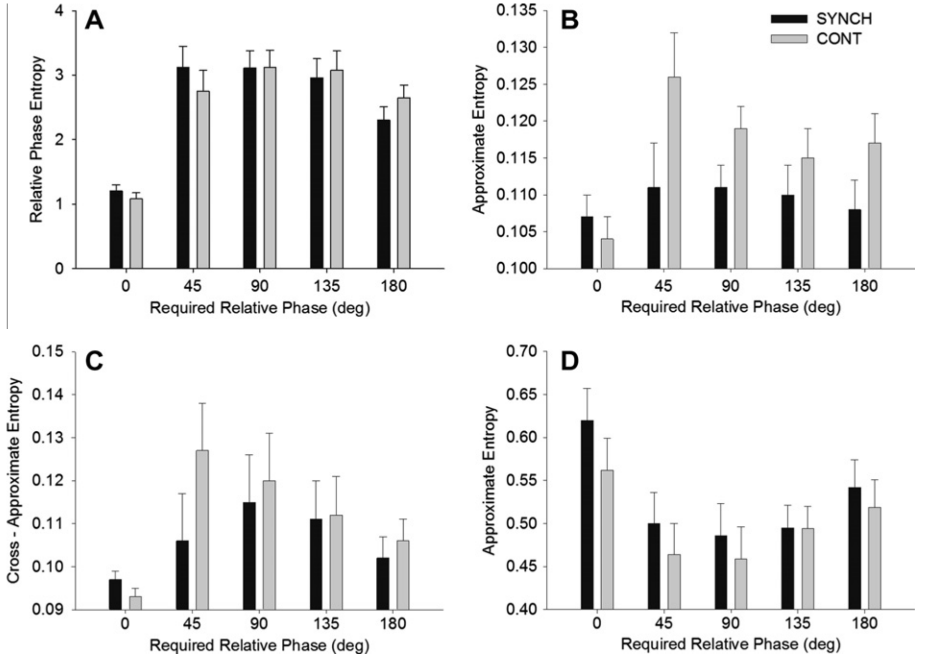

Fig. 2. Data are represented as functions of metronome group and relative phase condition. (A) Relative phase entropy. (B) Approximate Entropy of effectors. (C) Cross-Approximate Entropy of effectors. (D) Approximate Entropy of relative phase. SYNCH = Synchronization group; CONT = Continuation group. Standard errors are represented with error bars.

3.3. Effector Approximate Entropy

In effector ApEn data the main effect for metronome was not significant, $F(1, 18) = 1.68$, $p > .05$. There was a significant main effect for relative phase, $F(4, 72) = 5.97$, $p = .001$. In *post hoc* analysis the in-phase mode was significantly lower than all other relative phase modes (all $p < .05$). The antiphase mode was not significantly lower than any other modes. The 45° mode was significantly higher than the 135° ($p < .05$). There were no other significant differences between relative phase conditions (all $p > .05$).

The Relative Phase × Metronome interaction was significant, $F(4, 72) = 3.05$, $p < .05$. In *post hoc* analysis there were no significant differences between relative phase modes in the synchronization group (all $p > .05$) while significant differences between relative phase modes occurred in the continuation group (see Fig. 2B). In the continuation group the in-phase mode effector ApEn was lower than the antiphase, 45° (both $p = .001$), 90° ($p < .001$) and 135° ($p < .05$) modes. The antiphase mode was not significantly lower than any other modes (all $p > .05$). The 135° mode was lower than the 45° ($p = .01$). There were no other significant differences between relative phase conditions.

3.4. Cross-Approximate Entropy of effectors

In the Cross-ApEn of effectors the main effect for metronome was not significant, $F(1, 18) = 0.39$, $p > .05$. There was a significant relative phase condition effect, $F(4, 72) = 4.42$, $p < .01$ (see Fig. 2C). In *post hoc* analysis the in-phase mode was lower than antiphase ($p < .05$), 45°, 90° (both $p < .01$) and 135° ($p = .01$). There were no other significant differences between relative phase conditions (all $p > .05$). The Relative Phase × Metronome interaction was not significant, $F(4, 72) = 1.05$, $p > .05$.

3.5. Approximate Entropy of relative phase

The main effect for metronome was not significant, $F(1, 18) = 0.61$, $p > .05$. There was a significant main effect for relative phase condition (see Fig. 2D), $F(4, 72) = 8.02$, $p < .001$. In the *post hoc* analysis the in-phase mode was higher than the 45° ($p < .001$), 90° ($p = .001$), and 135° ($p < .01$) but was not significantly different than antiphase ($p > .05$). The antiphase mode was significantly higher than the 90° ($p < .01$) but did not differ significantly from 45° or 135° (both $p > .05$). There were no other significant differences between relative phase conditions (all $p > .05$) The Relative Phase × Metronome interaction was not significant, $F(4, 72) = 0.37$, $p > .05$.

4. Discussion

In the present study we tested the hypothesis of Newell and Vaillancourt (2001) that the dimensionality in bimanual coordination would be a function of performance level and the dimensionality of the task dynamic. We tested whether this hypothesis would apply simultaneously to the effector, coupling and task output levels of analysis with different dynamics operating on these levels. The hypothesis that the dimensionality in bimanual coordination would be a function of task performance and the dimension of the task dynamic at each level was supported by the direction of change across relative phase modes at each level of analysis and in each dependent variable.

We found that the highest level of task performance in bimanual coordination (of the in-phase mode) was characterized by lower effector and effector coupling dimensionality than lower level task performances found in all other coordination modes. This indicated that in the in-phase mode the neuromotor system was best able to adapt the motor dynamics to match the task demands of limit-cycle dynamics at these levels of analysis. The antiphase coordination mode was significantly higher in effector and coupling dimensionality than the in-phase mode. This reflected the intrinsically weaker stability of the antiphase attractor and lower level of task performance in this mode, in comparison to the in-phase attractor.

The antiphase mode was not significantly lower in effector or coupling dimensionality than the low level task performances of the 45°, 90° and 135° coordination modes. It was found that relative phase variability was lower in the antiphase mode than in two of the three unstable coordination modes. This indicated that the greater level of task performance and stability of the antiphase mode, in comparison to intrinsically unstable coordination modes, was evident at the level of the order parameter but not at the level of effector dynamics and the coupling of effectors.

The experimental hypothesis was also supported across relative phase modes at the task output level (relative phase) of analysis. At this level of analysis dimensionality was higher in the high level of task performances of the in-phase coordination mode than in the low level task performances of the unstable modes. This indicated that the neuromotor system was better able to adapt motor dynamics in the in-phase mode than in all other modes to meet the demands of the fixed-point task dynamics at this level of analysis. The antiphase mode was also found to have significantly higher dimensionality than one of the modes (90°) characterized by low task performance. A significant difference was found in the in-phase and antiphase dimensionality at the effector and coupling levels of analysis but not the task output (i.e., relative phase) level of analysis. This indicated that the greater level of task performance and stability of the in-phase coordination mode, in comparison to the antiphase, were more clearly observed at the two former levels of analysis than at the latter.

The combined findings in the dimensionality at the three levels of analysis were consistent with the theory that motor behavior is organized by constraining degrees of freedom (Bernstein, 1967; Kugler et al., 1980, 1982; Turvey, 1977, 2007) to meet task demands to a high degree. In the present study, the coordination mode (in-phase) characterized by the most highest levels of performance also had both the most highly constrained effectors and also the highest dimensionality in task output.

The absence of a main effect for metronome in any variable was consistent with the prior finding that an auditory metronome did not enhance the stability of an intrinsically unstable coordination mode (Maslovat et al., 2009). However, prior research found that auditory metronome tones led to increased local and global relative phase stability in the in-phase and antiphase coordination modes

(Fink et al., 2000). This led us to expect a significant Metronome × Relative Phase interaction in relative phase entropy (and potentially in the other dependent variables). The absence of a significant interaction in relative phase entropy is likely reflective of the relative weakness of the stability afforded by this behavioral information, in comparison to the greater differences in stability across relative phase modes.

The finding that there was a significant Metronome × Relative Phase interaction in effector ApEn, despite the absence of a significant interaction in relative phase entropy, indicated that the behavioral information had a greater impact on the dimensionality of effector movements than on the variability of relative phase. Without behavioral information during movement the in-phase mode was lower in dimensionality than all other modes. The presence of behavioral information led to decreased effector movement dimensionality in the antiphase and unstable modes such that there was no significant difference between these and the in-phase mode. This supported the hypothesis that the metronome group would produce lower effector movement dimensionality.

However, the present findings regarding behavioral information stand in contrast to prior research that found no anchoring effect in the unstable 90° mode (Maslovat et al., 2009). We suggest that while an auditory metronome may not provide an anchoring effect, in terms of a reduction in relative phase variability, in unstable coordination modes, the metronome appeared to produce a positive effect on the dimensionality of effector movements in the unstable coordination modes.

In summary, the present study supported the hypothesis of Newell and Vaillancourt (2001) that high level of task performance with limit-cycle dynamics is associated with low dimensionality while lower level task performance is associated with high dimensionality. The theoretical reason for this is that high level task performance in bimanual coordination is characterized by better adapting the motor system dynamics to better match the demands of the limit-cycle task demands. In the present study this consisted of decreasing the dimensionality of the effector movements and of the coupling between the effectors.

The results also supported the hypothesis that in task goals characterized by fixed-point dynamics this association is reversed, with higher dimensionality associated with low levels of performance. The task goal typically used in bimanual coordination studies (such as the present experiment) consists of producing a constant relative phase relation between effectors. Consistent with the Newell and Vaillancourt (2001) hypothesis the present study found that the motor system achieves this task goal by increasing the dimensionality of relative phase. The presence of behavioral information tended to reduce dimensionality only in effector movements. The present findings extended the hypothesis of Newell and Vaillancourt to apply across levels of analysis. Higher dimensionality was associated with high levels of performance at the level of task output, which possessed fixed-point dynamics, and lower dimensionality was associated with high levels of performance at the component and coupling levels of analysis, which had limit-cycle dynamics.

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