Learning and transfer in motor-respiratory coordination

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ABSTRACT

Motor-respiratory coordination occurs naturally during exercise, but the number of coordination patterns performed between movement and breathing is limited. We investigated whether participants could acquire novel ratios (either 5:2 or 5:3). To examine complex temporal relationships between movement and breathing, we used lagged return plots that were produced by graphing relative phase against relative phase after a time delay. By the end of practice, participants performed 5:2 consistently and performed 5:3 using more stable ratios (3:2 and 2:1). Lagged return plots revealed that 5:3 learners harnessed the stable inphase and antiphase patterns to stabilize the required ratio. That strategy resulted in the performance of smaller-integer ratios in the production of 5:3 but not 5:2. Despite those differences, there was positive transfer to unpracticed ratios that was similar in both learning conditions. The time series analysis of lagged return plots revealed differences in ratio performance at transfer. Ratios whose component frequencies were farther apart, like 7:2, were performed consistently, while ratios whose component frequencies were more similar, like 5:4, elicited attraction to inphase and antiphase. The implication is that participants can combine more stable chunks of rhythmic behavior to produce more complex ratios.

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1. Introduction

Motor-respiratory coordination, the synchronization of movement and breathing, occurs naturally during exercise. Synchronization can be defined by either consistent relative phasing (alignment of positions in the movement and breathing cycles) or the performance of particular frequency ratios (movement cycles produced per breath). Because the frequency of movement is usually faster than the frequency of breathing, the motor-respiratory coordination literature has focused primarily on the frequency ratios used. Across exercises, motor-respiratory coordination is limited to a small number of frequency ratios. The most commonly performed ratios are 2:1, 3:1, and 4:1 (Amazeen, Amazeen, & Beek, 2001; Bramble & Carrier, 1983; Garlando, Kohl, Koller, & Pietsch, 1985; MacDonald, Kirby, Nugent, & MacLeod, 1992; van Alphen & Duffin, 1994). Previous studies also have documented spontaneous and intentional ratio shifts (e.g., 4:1 to 2:1) in which breathing frequency is varied to accommodate changes in movement frequency (Bernasconi & Kohl, 1993; Bramble & Carrier, 1983; Garlando et al., 1985) and to vary the strength of coupling between movement and breathing with athletic demand (Garlando et al., 1985). Changes in breathing frequency have, therefore, been characterized as an internal pulmonary gearing mechanism (Bramble & Carrier, 1983; Garlando et al., 1985). Athletic flexibility could benefit from a larger repertoire of ratios that provides more efficient access to additional movement frequencies and an improved ability to accommodate athletic demands. Learning in motor-respiratory coordination has not been examined previously with the exception of one study in which novice rowers acquired 1:2 (Mahler, Hunter, Lentine, & Ward, 1991), a ratio that develops naturally with practice and is commonly used by elite rowers. The current study was designed to investigate the learning of ratios that would not normally be acquired through training.

1.1. Important findings on learning dynamics

An extensive literature exists on learning in another type of coordination between two rhythmic processes, interlimb coordination, in which the components are movements of the limbs (e.g., arms, legs) or limb segments (e.g., fingers, hands). The interlimb coordination literature is, therefore, a reasonable starting place to inform the study of learning in motor-respiratory coordination. In interlimb coordination, most participants exhibit bistability, performing two relative phase patterns in a stable manner without practice: inphase (0°), when symmetric muscles flex and extend simultaneously; and the slightly less stable antiphase (±180°), when symmetric muscles flex and extend alternately (Haken, Kelso, & Bunz, 1985; Kelso, 1984). The latest research suggests that multistability, stable performance of inphase, antiphase, and the gallop (90°), in which one limb leads the other by ¼ cycle, is exhibited by about 25% of the population (Kostrubiec, Zanone, Fuchs, & Kelso, 2012). Other relative phase patterns that are not performed naturally can be learned (Kostrubiec, Tallet, & Zanone, 2006; Kostrubiec et al., 2012; Zanone & Kelso, 1992a,b; Zanone, Kostrubiec, Albaret, & Temprado, 2010). Zanone and Kelso (1992a) used a probe procedure to examine the learning of 90° by bistable participants in which they mimicked relative phase relations from 0° to 180° in 15° increments as prompted by a visual metronome. Probes early in learning revealed that participants approximated 90° from the direction of 180°, which provided a stable position from which to anchor learning but enough flexibility to allow for change in behavior. The first important learning finding is that existing, naturally stable coordination patterns can influence the acquisition of novel coordination patterns (Kostrubiec et al., 2006, 2012; Zanone & Kelso, 1992a,b; Zanone et al., 2010).

Zanone and Kelso (1992a,b) also identified that the acquisition of 90°, in turn, reduced the accuracy and stability of 180° performance, although later studies suggested that the effect was temporary (Fontaine, Lee, & Swinnen, 1997; Lee, Swinnen, & Verschueren, 1995). That is, there was at least a temporary negative transfer effect in which practice of a novel coordination pattern was a detriment to the performance of an existing coordination pattern. Positive transfer has also been observed in interlimb coordination in which practice on one coordination pattern can benefit the performance of other coordination patterns. In one study, participants practiced either +90° (right-leads-left) or −90° (left-leads-right) (Zanone & Kelso, 1997). After 50 trials of learning, a probe was performed. Acquisition of either +90° or −90° led to an increase in stability of the unpracticed, opposite lead, gallop pattern. The second

important learning finding is that practice of one coordination pattern can result in transfer to other, unpracticed coordination patterns (Fontaine et al., 1997; Lee et al., 1995; Zanone & Kelso, 1992a,b, 1997).

1.2. Order parameters

The order parameter—a quantitative measure of the state of a system—in the interlimb coordination studies above was the relative phase of limb movements. It was defined on a moment-by-moment basis as the location in the cycle of one oscillator relative to the location in the cycle of another oscillator. Relative phase is typically used to describe 1:1 coordination in which the component frequencies are the same. In some interlimb coordination skills like drumming, the component frequencies are usually different and, thus, exhibit multifrequency relationships like 3:2, 2:1, and 3:1 (Peper, Beek, & van Wieringen, 1991, 1995a,b; Treffner & Turvey, 1993). Motor-respiratory coordination also fits into that multifrequency category. For example, in exercises like walking (van Alphen & Duffin, 1994), running (Bernasconi & Kohl, 1993; Bramble & Carrier, 1983), and manual wheelchair propulsion (Amazeen et al., 2001), the frequency of movement is generally faster than the frequency of breathing. In rowing, the multifrequency relationship is reversed because the length of the oar makes the frequency of the rowing stroke slower than the frequency of breathing (Mahler et al., 1991). The order parameter typically used to describe drumming and motor-respiratory coordination is the frequency ratio.

It is also possible that multifrequency coordination may manifest itself at particular relative phases (de Guzman & Kelso, 1991). In that way, multifrequency coordination is reflected in the relative phase regime. To illustrate, a performance template for 5:2 is presented in Fig. 1, Panel A. Performance templates have been shown to facilitate the performance of complex ratios in coordination between arm movement and breathing (Hessler, Gonzales, & Amazeen, 2010). The performance template is composed of horizontal lines for breathing and movement with hash marks that identify inhalation onsets and forward-most arm movements. Notice that the first breathing and movement hash marks are aligned (an inphase relation) and that the second breathing hash mark is halfway between two movement hash marks (an antiphase relation). During performance, individuals may try to anchor breathing and movement, as much as possible, at those landmarks than at other parts of a ratio cycle. That synchronization could be accomplished by slowing down or speeding up a component's frequency (movement or breathing) within a ratio cycle.

1.3. Sine circle map

The ratios observed in motor-respiratory coordination (most often 2:1 and 3:1) are consistent with observations in interlimb coordination (de Guzman & Kelso, 1991; Deutsch, 1983; Haken, Peper, Beek,
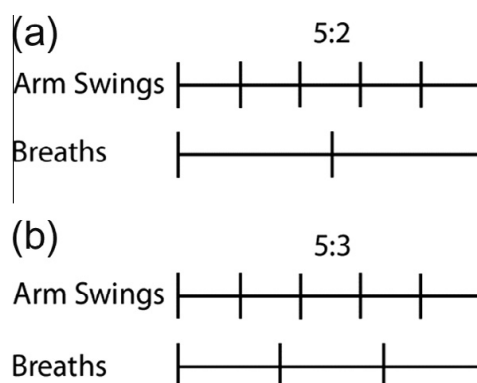
Fig. 1. Static performance templates were presented to facilitate ratio performance during practice and probe trials. Performance templates for the 5:2 (a) and 5:3 (b) ratios are depicted. The upper lines in each template represent arm movement and the lower lines represent breathing. Hash marks on the arm movement lines indicate the location of forward-most arm movements, while hash marks on the breathing lines indicate inhalation onsets.

& Daffertshofer, 1996; Peper et al., 1991, 1995a,b; Treffner & Turvey, 1993) and with the predictions of a dynamical model called the *sine circle map* (Glass & Mackey, 1988; González & Piro, 1985; Jensen, Bak, & Bohr, 1984; Schroeder, 1991),

$$\theta_{n+1} = \theta_n + \Omega + \frac{K}{2\pi} \sin(2\pi\theta_n), \tag{1}$$

which has been used to identify regions of stability in the coordination of any two oscillators (Bak, 1986). θ_n is the phase angle of an oscillation strobed at regularly-spaced intervals. The next phase angle, θ_{n+1}, is a function of three factors: (a) θ_n, the current phase angle; (b) Ω, the *bare winding number*, or ratio of uncoupled frequencies; and (c) nonlinear coupling of strength K between the oscillators. As modeled, coupling is unidirectional. We assume that unidirectionality holds for motor-respiratory coordination, as a unidirectional influence of movement on breathing has been suggested in the literature (e.g., Bramble & Carrier, 1983; Garlando et al., 1985).

Predictions may be made for *W*, the *dressed winding number*, which is defined as the observed ratio in an experiment. Predictions for *W* as a function of *K* and Ω are summarized via iteration of the sine circle map in the *Arnold tongues* (see Fig. 2; Arnold, 1965; Glass & Mackey, 1988; Schroeder, 1991). The white tongues are regions of stability; regions of instability are the black spaces between the white tongues. If initial conditions are within the boundaries of a tongue, then the system is attracted to the rational ratio associated with that tongue (Peper et al., 1995b). At a fixed *K*, Arnold tongue widths vary. The implication for performance is that ratios that reside in wider tongues are more stable because they can be performed across a wider variety of conditions. As *K* increases, all tongues become wider, crowding out regions of instability. At *K* = 1, there are no regions of instability. The potential implication for learning is that if *K* increases as a function of practice on any ratio, then the stability of performance of all other ratios will benefit.

Ratio stability, as specified in the Arnold tongues, can be rank ordered in a mathematical structure known as the *Farey tree*. The first five levels (Levels 0–4) of the Farey tree are presented in Fig. 3. In that rank ordering, which has been confirmed empirically in numerous behavioral experiments, ratio stability is inversely related to level number. In motor-respiratory coordination, performance was less variable for Level 2 ratios than for Level 3 or 4 ratios (Hessler et al., 2010), and 2:1 and 3:1 (lower-level ratios) were performed most frequently at moderate movement frequencies (Amazeen et al., 2001; Villard, Casties, & Mottet, 2005). Moreover, transitions were observed from higher-level (e.g., 5:3)
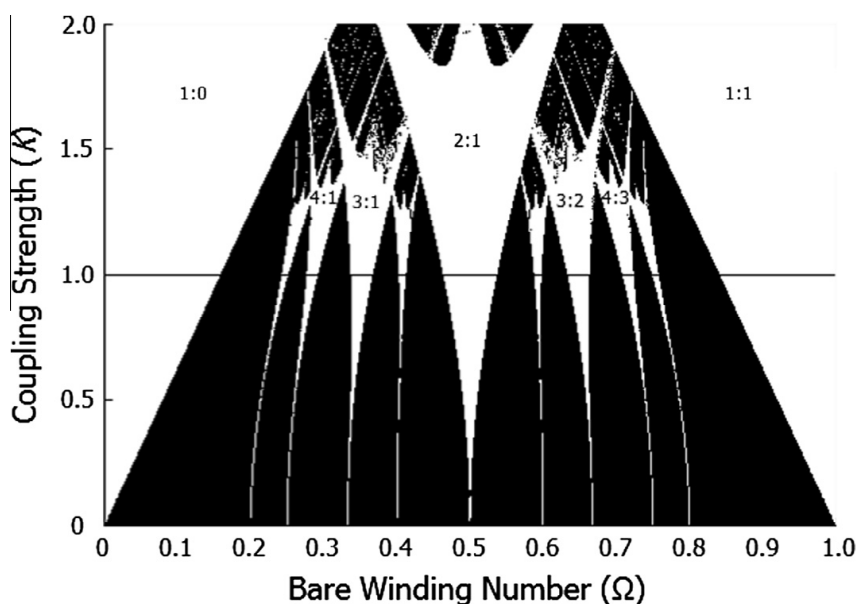

Fig. 2. The Arnold tongues simulated from the sine circle map; only tongues (white) for ratios through Level 4 of the Farey tree are depicted. Larger resonances are labeled with the corresponding frequency ratio. Behavior that falls within an Arnold tongue resonates toward the rational ratio corresponding to that tongue.
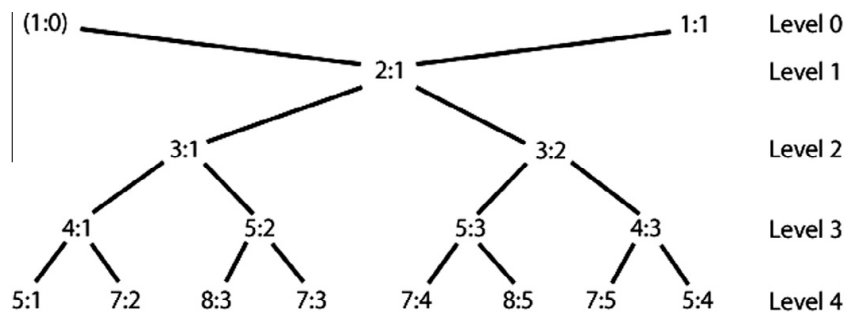
Fig. 3. The first five levels of the Farey tree (Levels 0–4). Note that lower-level ratios are depicted higher in the tree.

toward lower-level (e.g., 3:2) ratios in interlimb coordination (de Guzman & Kelso, 1991; Deutsch, 1983; Haken et al., 1996; Peper et al., 1991, 1995a,b; Treffner & Turvey, 1993) and motor-respiratory coordination (Villard et al., 2005), particularly at faster oscillation frequencies. The predominance of lower-level ratios in motor-respiratory coordination, as in interlimb coordination, is likely a function of ratio stability.

1.4. Learning, transition and transfer

In the current study, participants practiced either 5:3 or 5:2; two ratios from the same level of the Farey tree (Level 3). Both 5:3 and 5:2 are sufficiently high in the Farey tree for their performance to be considered difficult. Over practice, the performance of both patterns is expected to improve in terms of accuracy and stability (e.g., Zanone & Kelso, 1992a, 1994). However, early in learning, performance will likely transition to more stable ratios. Consistent with the dynamics specified in the sine circle map, transitions are most likely to occur from higher-level ratios toward lower-level ratios (de Guzman & Kelso, 1991; Haken et al., 1996; Peper et al., 1991, 1995a,b; Treffner & Turvey, 1993; Villard et al., 2005) and are likely to follow branches of the Farey tree (de Guzman & Kelso, 1991; Peper et al., 1991, 1995a,b; Treffner & Turvey, 1993; Villard et al., 2005). Therefore, transitions are expected to be toward so-called "parent" ratios in the Farey tree. For any two parent ratios $p_1:q_1$ and $p_2:q_2$, the ratio positioned between the two parent ratios is $(p_1 + p_2):(q_1 + q_2)$. Initial performance of 5:3 is expected to transition toward the more stable, lower-level ratios 3:2 and 2:1 (5:3's parent ratios), whereas transitions from 5:2 are expected to be toward 3:1 and 2:1 (5:2's parent ratios).

As indicated earlier, multifrequency coordination contains implicit relative phase relations. Recall the 5:2 performance template presented in Fig. 1, Panel A. At the landmarks in the template, both the inphase and antiphase patterns are embedded in perfect 5:2 performance. A performance template for 5:3 is presented in Fig. 1, Panel B. Notice that the second and third breathing hash marks are neither aligned with a movement hash mark nor are they located halfway between two movement hash marks. That is, at those landmarks in the template, neither inphase nor antiphase are embedded in perfect 5:3 performance. However, those stable relative phase relations may provide a starting position from which to anchor acquisition (e.g., Zanone & Kelso, 1992a,b). Participants could solve the problem of performing a novel pattern by shifting the second and third breaths slightly earlier, into antiphase and inphase relations with movement, respectively. Of course, those shifts would also result in the performance of the more stable 3:2 and 2:1 ratios, as opposed to the intended 5:3 ratio.

Transfer could be either general or specific depending on the impact of practicing the 5:3 or 5:2 ratios. Synchronization of movement and breathing requires communication across the two physiological subsystems. In the sine circle map, K captures the strength of this communication and is thought to underlie the performance of all ratios (Jagacinski, Peper, & Beek, 2000; Summers, 2000). Our hypothesis is that training on a specific ratio may serve to enhance the communication across the physiological subsystems of the body as captured by an increase in K. The implication regarding transfer is that learning one ratio will result in the stabilization of any unpracticed ratio (Jagacinski et al., 2000). If learning 5:3 or 5:2 increases overall K, then general positive transfer, as evidenced by increases in the accuracy and stability of the performance of any unpracticed ratio, is expected.

The alternate hypothesis is that transfer will not be general because particular frequency and relative phase relations are associated with the performance of each ratio. One possibility is that participants may become more skilled at establishing *W*. That is, they may gain more refined control over the practiced frequency relation only. Another possibility, proposed by Jagacinski et al. (2000), is that models with a single coupling term are ill-suited to address learning. They proposed using a model with multiple coupling terms, such as the one proposed by Haken et al. (1996), but modified so that each coupling term would encompass several related ratios. In that type of model, more specific positive transfer would be expected than is predicted from the sine circle map. Assuming that related ratios are those with more similar frequency and relative phase relations, specific positive transfer would be evidenced by increases in the accuracy and stability of the performance of ratios along the same branch of the Farey tree. We adapted the probe procedure used by Zanone and Kelso (1992a,b, 1994) for interlimb coordination to test for transfer in motor-respiratory coordination. Probes were introduced to evaluate ratio performance before learning, to examine transfer after learning, and to determine whether or not transfer was robust over a one-week retention interval.

2. Method

2.1. Participants

Twenty-one participants (7 men, 14 women; 19–34 years old; 20 right-handed, 1 left-handed) volunteered or received credit toward their introductory psychology course to participate. They all had full use of their shoulders and arms, were not experiencing any respiratory difficulties, and did not smoke. Participants were randomly assigned to one of two practice groups: either 5:2 or 5:3. Ten participants practiced 5:2 and eleven practiced 5:3. One 5:2 participant did not return for the retention test. The movement data for one 5:3 participant were occluded from view of the movement tracking device during a later learning trial and were, therefore, excluded from the analysis. All participants were treated in accordance with the ethical principles of the American Psychological Association.

2.2. Apparatus

The task, which required coordination between arm movement and breathing, was similar to that used in previous studies (Gonzales, Hessler, & Amazeen, 2010; Hessler & Amazeen, 2009; Hessler et al., 2010). While the task involves weaker mechanical and energetic constraints than other types of motor-respiratory coordination (e.g., running and rowing), expected differences in ratio performance are exhibited by participants performing the task such as an inverse relationship between a ratio's Farey tree level and its stability. Each participant sat in a chair and swung the preferred arm forward and backward in the sagittal plane. Movement was constrained with elbow and wrist restraints to ensure rotation of the shoulder joint only. A 1.36 kg weight was held in order to increase the pendular quality of arm movement (to smoothen the trajectory). To encourage consistent arm movement amplitude, two flags were placed 30 cm to the front and back of the arm. Participants paced arm movement to a 0.67 Hz metronome, which was a comfortable frequency used for interlimb coordination (e.g., Treffner & Turvey, 1993). Participants were instructed to tap the front flag at each metronome tone. Arm movement frequency approximated the prescribed frequency during learning ($M = 0.67$ Hz) and probe ($M = 0.67$ Hz) trials.

Breathing was paced with movement to establish the required ratios. Static performance templates were displayed on a computer monitor that was positioned 2.4 m in front of each participant (see also Hessler et al., 2010). In the current study, performance templates were used during both learning and probe trials. The performance templates for 5:2 (Panel A) and 5:3 (Panel B) are presented in Fig. 1. The participants' task was to establish a consistent arm swing at the metronome frequency and add breaths to the arm swing as prompted by each breath hash mark. Participants were instructed to inhale and exhale as evenly and as naturally as possible. No feedback or knowledge of results were provided. During learning trials, a performance template for either 5:2 or 5:3 was depicted. During probe trials, a performance template for each ratio was depicted, one at a time, through Level 4 of the Farey

tree: 1:1, 2:1, 3:1, 4:1, 5:1, 3:2, 4:3, 5:2, 5:3, 5:4, 7:2, 7:3, 7:4, 7:5, 8:3, and 8:5 (randomized presentation).

An Optotrak/3020 (Northern Digital, Waterloo, Canada) that was positioned 2.4 m in front of each participant was used to collect movement data. Forward/backward arm movements about the shoulder occurred in the sagittal plane. Raising the arm away from the body in the coronal plane marked the probe data to indicate a change from one ratio to the next. An Oxycon Alpha (Erich Jaeger Company, Bunnik, The Netherlands) registered breathing using a spinning turbine mounted in a mouthpiece. The mouthpiece was attached to a facemask that was worn over the nose and mouth. Collection of movement and breathing data was synchronized, and the sampling rate was 25 Hz.

2.3. Procedure

The experimental procedure is depicted in Fig. 4. There were two types of experimental blocks: probe and practice. During each probe block, the order of ratio presentation was random. Each ratio was performed for 30 s with a 5-s rest before the next ratio. To ensure that only sagittal arm movements would be analyzed, data from both 2 s before and 3 s after the coronal arm movement were eliminated. After every fourth ratio, participants rested for 30 s to minimize fatigue. That pattern of ratio performance and rests continued until all 16 ratios were completed. Each practice block consisted of 20 trials. During each practice trial, participants practiced five arm movements to either three breaths (5:3) or two breaths (5:2) for 60 s. There was a minimum 30-s rest between each practice trial with more rest provided upon request to minimize fatigue.

Testing occurred over a period of three days. Probes were conducted before practice, after practice, and after a one-week retention interval. As identified in Fig. 4, Day 1 consisted of one probe block followed by one practice block. Participants returned 24 hours later for one practice block followed by one probe block. One week after Day 2, participants returned for a cued recall of the practiced ratio followed by one probe block. For the cued recall, a performance template of the practiced ratio appeared on the monitor for 20 s, during which time participants were told not to perform the ratio. We then turned off the monitor and turned on a metronome at 0.67 Hz. Participants performed the practiced ratio without the performance template for 60 s.

2.4. Calculations

A 5-point running average was computed to smooth raw movement and breathing data. The derivative of smoothed breathing data was calculated and maxima were obtained. Maxima represented the fastest inhalation velocities and were defined as inhalation onsets. Arm movement frequencies were calculated by dividing the 25 Hz sampling rate by the difference in timing between successive arm movement maxima (forward-most positions). Breathing frequencies were calculated similarly but using the timings associated with breathing maxima. A cycle-by-cycle frequency ratio was then calculated at each breath by dividing movement frequency by the corresponding breathing frequency. The decimal equivalents for the learned ratios were: 5:3 = 1.67 and 5:2 = 2.50. The decimal equivalents for the other probed ratios were: 1:1 = 1.00; 5:4 = 1.25; 4:3 = 1.33; 7:5 = 1.40; 3:2 = 1.50; 8:5 = 1.60; 7:4 = 1.75; 2:1 = 2.00; 7:3 = 2.33; 8:3 = 2.67; 3:1 = 3.00; 7:2 = 3.50; 4:1 = 4.00; and 5:1 = 5.00. Measurements need to be precise to differentiate between neighboring ratios. In Appendix A, we characterize measurement error based on the 25 Hz sampling rate. The greatest possibility for ratio confusion is between 8:5 and 5:3. If the 8:5 calculation is overestimated and the 5:3 calculation is underestimated, then 8:5 or 5:3 could be misinterpreted for each other. Measures of accuracy, or
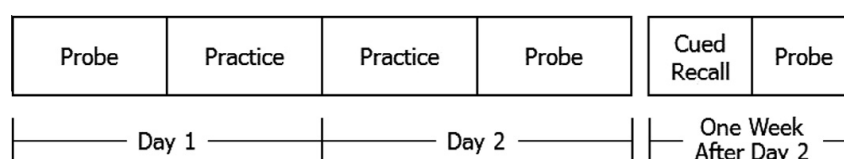

Fig. 4. Schematic of the experimental procedure.

constant error (CE), and variability, or variable error (VE), were calculated from the cycle-by-cycle frequency ratio. CE was the average difference between the performed and intended frequency ratio (performed−intended) over a trial. VE was the standard deviation of the performed frequency ratio over a trial.

We also performed a calculation of continuous relative phase. Smoothed movement and breathing data were plotted against their first derivatives to create phase plots (position × velocity). Continuous relative phase was the difference between the movement and breathing phase angles (movement−breathing). In contrast to 1:1 coordination, all relative phases are traversed in multifrequency coordination. We used the following conventions: (a) positive relative phase indicated that movement led breathing within each cycle; (b) negative relative phase indicated that breathing led movement within each cycle; (c) inphase (0°) indicated that forward arm movements were synchronized with inhalations and backward arm movements were synchronized with exhalations; and (d) antiphase (±180°) indicated that forward arm movements were synchronized with exhalations and backward arm movements were synchronized with inhalations.

3. Results

3.1. Frequency ratio learning and retention

It is standard practice in the learning literature to examine mean behavior, with the expectation that accuracy (called CE here) will improve and variability (called VE here) will decrease over the course of learning. We examined mean behavior first and then considered patterns in the individual time series. Fig. 5 depicts frequency ratio CE (Panel A) and VE (Panel B) for the 5:2 (dashed line) and 5:3 (solid line) practice conditions. Acquisition was examined using 2 (Practice Condition: 5:2, 5:3) × 40 (Trials) mixed analyses of variance (ANOVAs). There were significant effects of Trial on both CE, $F(39, 702) = 2.19$, $p < .001$, and VE, $F(39, 702) = 2.40$, $p < .001$. The data were evaluated for exponential decay across practice using linear regression (Cohen, Cohen, West, & Aiken, 2003). Exponential decay fits the equation

$$Y = ce^{dX}. \tag{2}$$

That equation can be linearized by taking the logarithm of each side, which yields

$$\log Y = dX + \log c. \tag{3}$$

We fit our data to Eq. (3) using regression analyses, where Y was either CE or VE and X was Trial. To avoid taking logarithms of negative numbers, it was necessary to add 1.0 to each CE value. The following regression equations resulted from the analyses:

$$\log(CE + 1) = -0.0009 \text{ Trial} + 0.0335 \tag{4}$$
$$\log(VE) = -0.0051 \text{ Trial} - 0.5314. \tag{5}$$

Trial was a significant predictor of both $\log(CE+1)$, $t(837) = 4.30$, $p < .001$, $R^2 = .02$, and $\log(VE)$, $t(837) = 6.54$, $p < .001$, $R^2 = .05$, which indicates that there was greater improvement at the start of practice than at the end of practice.

Neither the main effects of Practice Condition on CE, $F(1, 18) = 3.44$, $p > .05$, and VE, $F(1, 18) = 0.27$, $p > .05$, nor the interactions involving Practice Condition on CE, $F(39, 702) = 0.65$, $p > .05$, and VE, $F(39, 702) = 1.05$, $p > .05$, were significant in the omnibus ANOVAs. Those results suggest that patterns of accuracy and variability were similar during the acquisition of 5:2 and 5:3. A t-test comparing 5:2 CE, $t(9) = 0.26$, $p > .05$, and 5:3 CE, $t(10) = 2.18$, $p > .05$, to zero for the average of the last four learning trials indicated that performance approximated the intended ratios. Separate 2 (Practice Condition: 5:2, 5:3) × 2 (average of last four learning trials versus recall trial) ANOVAs on CE and VE produced no significant Trial effects. The accuracy and consistency of ratio performance at the end of practice was retained for one week.
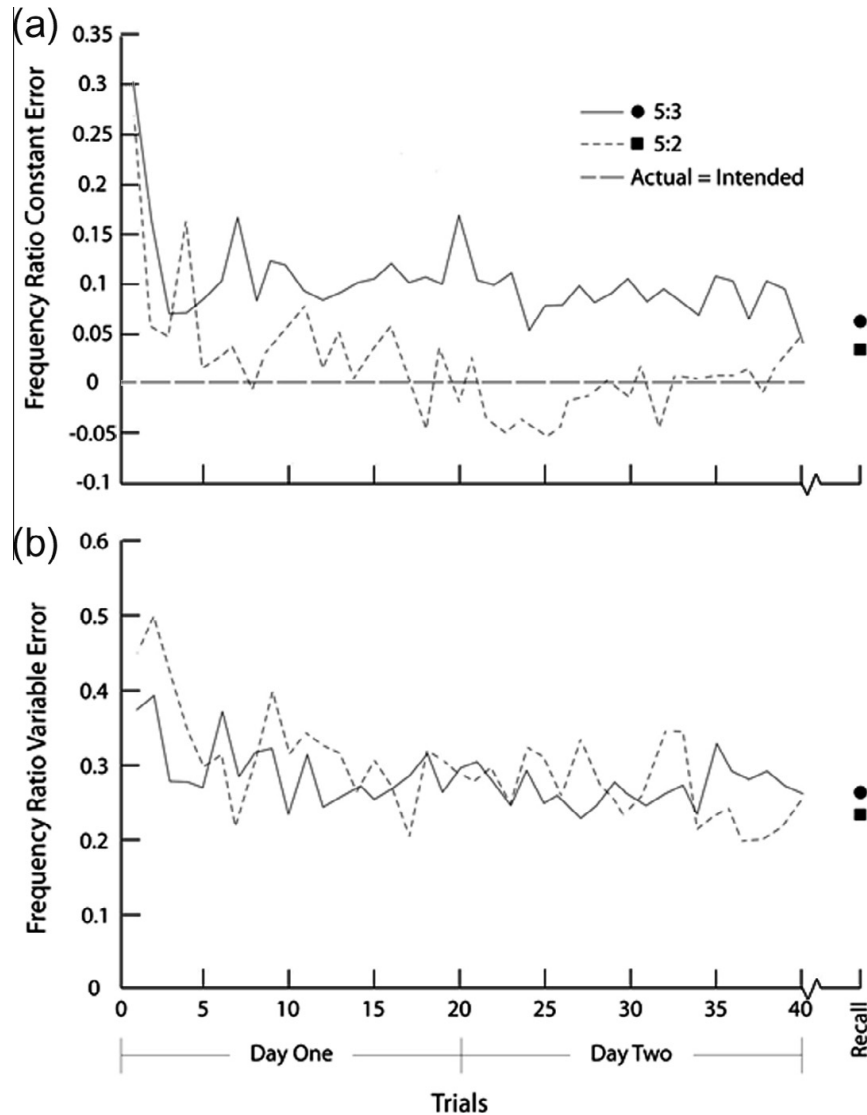
Fig. 5. Mean frequency ratio constant error (a) and variable error (b) as a function of practice condition (5:3 and 5:2). Learning trends over two days of practice and performance at recall are depicted. The long dashed line indicates where the performed frequency ratios equal the intended frequency ratios.

3.1.1. Differences in frequency ratio performance

Differences in 5:2 and 5:3 performance were not evident in the means for CE and VE, but they were clear in the individual time series. Fig. 6 depicts 30 s time series from Trial 40 (the last practice trial) for participants in the 5:2 (Panel A) and 5:3 (Panel B) conditions. Positive slopes represent forward arm movements and inhalations, and negative slopes represent backward arm movements and exhalations. Notice that participants performed five arm movements (dashed line) and either two (Panel A, 5:2 condition) or three (Panel B, 5:3 condition) breaths (solid line) per frequency ratio cycle. Arm movement appears to be consistent for both 5:2 and 5:3 performance, whereas breathing appears to be more consistent for 5:2 than for 5:3. Specifically, the first two breaths of each 5:3 cycle look similar in appearance, and the third breath looks longer. This suggests graphically a pattern of *chunking*, a term that is widely used in cognitive psychology to describe the tendency to cluster similar items so as to better retain them in memory. In the apparent chunking pattern observed here, the performance of 5:3 appears to be composed of patterns of smaller-integer ratios (i.e., 3:2 and 2:1) from lower levels of the Farey tree.

We produced histograms (bin size = 0.125) that summarized ratio performance at Trial 40 of learning across participants. The percentage of cycles spent performing different ratios when participants were instructed to perform 5:2 (filled bar) or 5:3 (open bar) is depicted in Fig. 7. The number of cycles
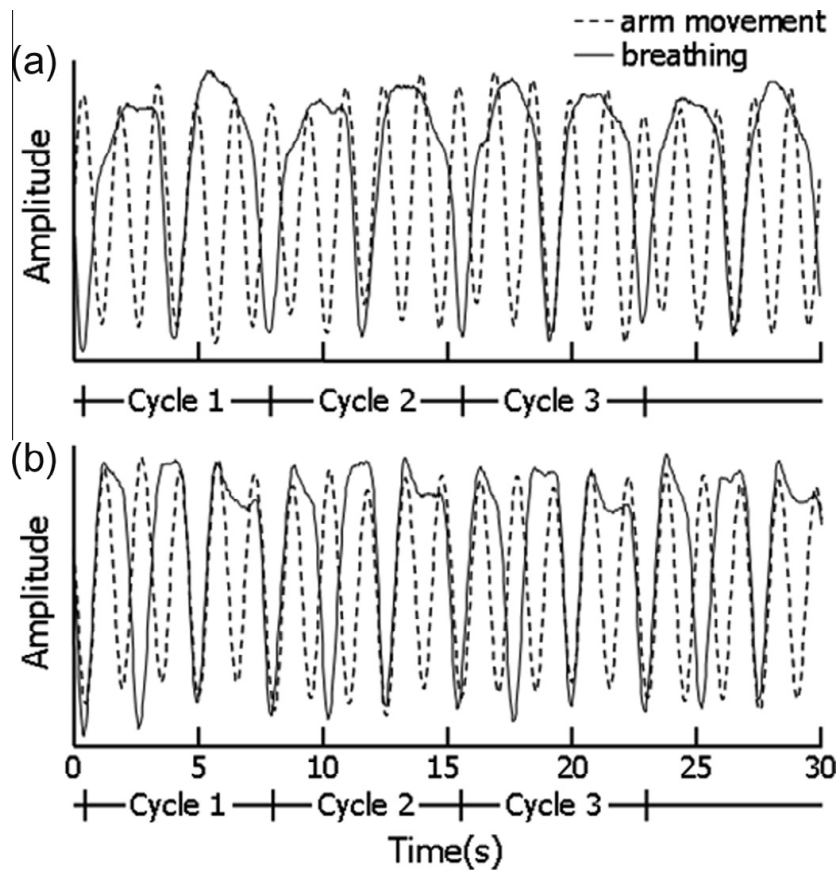
Fig. 6. Time series from Trial 40 of practice depict the relationship between arm movement and breathing for representative participants in the 5:2 (a) and 5:3 (b) practice conditions.
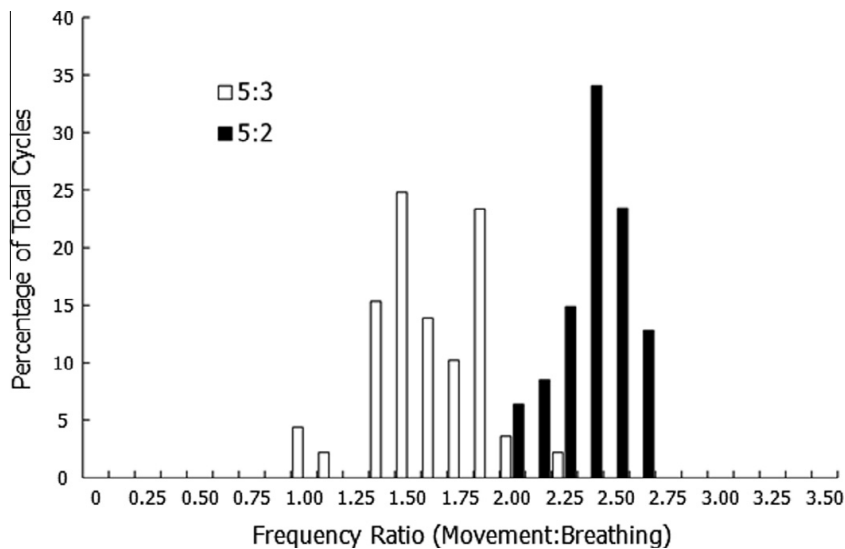
Fig. 7. Frequency ratio histograms (bin size = 0.125) as a function of practice condition (5:2 and 5:3) produced using data from Trial 40 of practice for all participants.

under each peak was calculated by adding the total number of cycles performed within ±0.125 of each local maximum. The 5:2 histogram is unimodal: there is one large peak at the 2.375 frequency ratio bin. In contrast, the 5:3 histogram is bimodal: there are larger peaks at the 1.5 and 1.875 frequency ratio bins. Those peaks approximated for the learning groups the ratios observed in the individual 5:2 (5:2 = 2.5) and 5:3 (3:2 = 1.5 and 2:1 = 2.0) time series (see Fig. 6).

3.1.2. Differences in relative phase substructure

One explanation for the observed chunking behavior is that participants were synchronizing their motor-respiratory patterns so as to take advantage of the stability offered by component inphase and antiphase patterns. In the time series of Fig. 6, attraction to inphase (0°) and antiphase (±180°) is manifest as the synchronization—either in the same direction (inphase) or in opposite directions (antiphase)—of movement (dashed line) and breathing (solid line) cycles. There appears to be slightly more attraction to inphase and antiphase for 5:3 (Panel B) than for 5:2 (Panel A), but there is a way to examine this possibility that is more principled than the visual inspection of time series plots. We used a novel procedure, called *lagged return plots*, to examine the role of inphase and antiphase performance in the performance of these multifrequency ratios. We calculated continuous relative phase at time t, producing one relative phase value for each pair of movement and breathing data points in the time series. We then calculated continuous relative phase at time $t + \tau$ (after a time delay). The time delay (τ) was the first zero crossing of the breathing autocorrelation function (equivalent to about $\frac{1}{4}$ cycle). It is the point, on average, at which observations in the time series are maximally independent (Takens, 1981). A lagged return plot is a plot of relative phase$_t$ against relative phase$_{t+\tau}$.

Lagged return plots from Trial 40 of practice for the representative 5:2 (top row, left panel) and 5:3 (top row, right panel) participants are depicted in Fig. 8. A line of identity (solid diagonal line) drawn across each panel represents relative phase, unchanged over the time delay. We were interested in how relative phase changed over the time delay. For idealized ratio performance, in which the correct component frequencies would be maintained during an entire trial, the change from relative phase$_t$ to relative phase$_{t+\tau}$ would be consistent over all values of t (represented by the dashed diagonal line in each plot). Effectively, relative phase values would constantly drift upward, off of the line of identity toward the dashed diagonal line; note that phase wrapping produces a natural wrap-around effect.

For this 5:2 learner (top row, left panel), data points clustered around that dashed diagonal line. That indicates near-perfect 5:2 performance, with consistent upward drift in relative phase values throughout the trial. Although local attraction to inphase and antiphase may be apparent in Fig. 6,

Fig. 8. Lagged return plots from Trial 40 of practice (top row) depict the evolution of relative phase over a time delay (τ) for representative participants in the 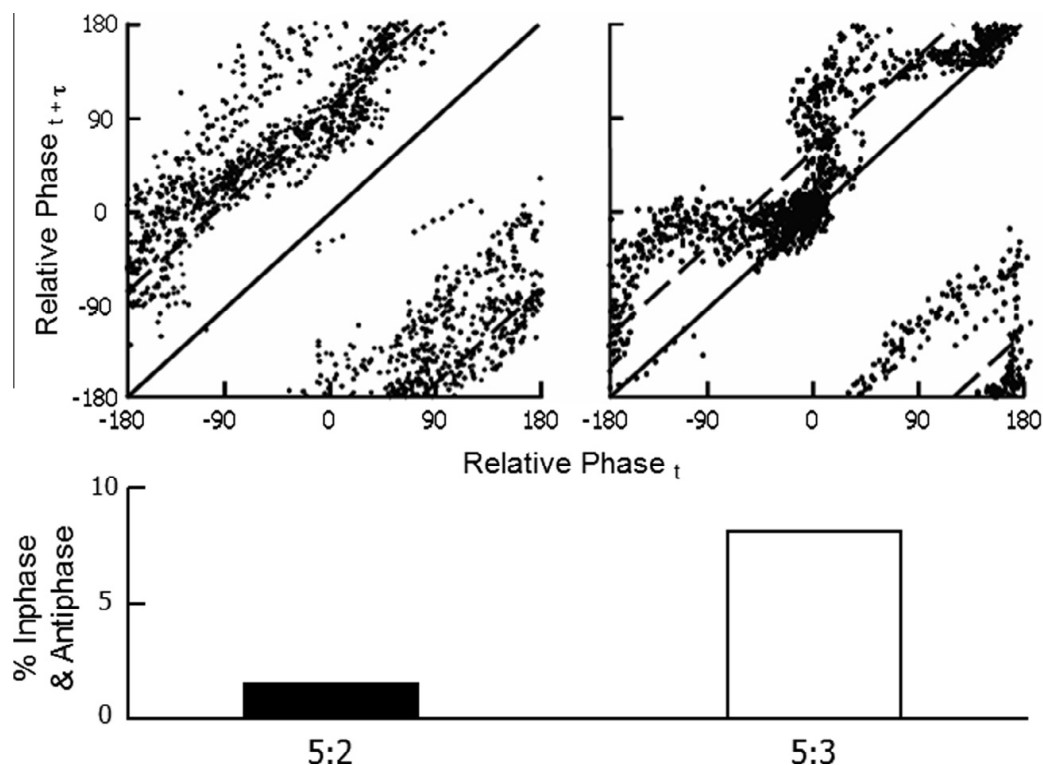5:2 (left panel) and 5:3 (right panel) practice conditions. The percentage of points around inphase and antiphase (bottom panel) as a function of practice condition (5:2 and 5:3) for all participants.

Panel A, for 5:2 performance, this attraction is brief relative to the frequency of breathing, so it is not detected in the analysis. The 5:3 learner demonstrated a different strategy (top row, right panel). Data points clustered at 0° relative phase$_t$ and relative phase$_{t+\tau}$, and ±180° relative phase$_t$ and relative phase$_{t+\tau}$. That is, performance dwelled at inphase and antiphase, resulting in an overall 5:3 pattern, but that overall pattern was clearly broken into chunks that exploited intrinsic relative phase stability. There is no way to extract the component frequency ratios from the lagged return plot; we must examine the time series and histograms to recognize that 5:3 learners are combining 2:1 and 3:2 in their production of the overall 5:3 pattern.

To examine the use of these different strategies for all 5:2 and 5:3 learners, we produced lagged return plots for all participants and then calculated the percentage of data points within ±30° of inphase and antiphase. Fig. 8 (bottom panel) depicts those percentages for the 5:2 (filled bar) and 5:3 (open bar) practice conditions. The main effect of Practice Condition on the percentages, $F(1, 18) = 12.12$, $p < .01$, was significant in a one-way ANOVA. That result supports for the learning groups the observation made in individual lagged return plots that attraction to the intrinsic relative phase dynamics of inphase and antiphase was stronger for 5:3 than for 5:2. Together with the frequency ratio histograms (see Fig. 7), those results suggest that learning varied with the instructed ratio: participants learned 5:2 and performed 5:3 by piecing together the smaller-integer ratios of 2:1 and 3:2. Those smaller-integer ratios are lower-level ratios along the same branch of the Farey tree as 5:3.

3.2. Probes revealed positive transfer

We next examined transfer by analyzing improvements in both performance accuracy and consistency followed by whether the observed chunking strategy persisted during transfer to other ratios. We compared performance on the 16 Farey tree ratios during probes before learning, after learning, and after a one-week retention interval. As with the analysis of learning, positive transfer is indicated by improved accuracy (CE approaches zero) and consistency (VE decreases). Mean frequency ratio CE across all 16 ratios is depicted in Fig. 9 for the 5:2 (Panel A) and 5:3 (Panel B) practice conditions. Notice that the functions appear rather linear before learning (solid line) and appear to take on a negative cubic form both after learning (short dashed line) and at retention (dotted line). Those changes are representative of positive transfer. We will explain the meaning of each function following their statistical verification.

We used polynomial regression to quantify changes in the functions for the 5:2 and 5:3 practice conditions before learning, after learning, and at retention. In each regression equation, we used the original, squared, and cubed intended ratios as predictors of CE to test for linear, quadratic, and cubic relationships, respectively:

$$CE_k = \beta_1(\text{intended}_r) + \beta_2(\text{intended}_r)^2 + \beta_3(\text{intended}_r)^3 \tag{6}$$

where the dependent variable CE for each individual, k, was predicted by the intended ratios, r. β_1, β_2, and β_3 were the slopes of the linear, quadratic, and cubic relationships, respectively. Although the intended ratios in Fig. 9 are uncentered, analyses were performed with centered intended ratios to provide the correct interpretation of lower-order terms.

Table 1 depicts the results of the regression analyses. *T*-tests for each β represent the significance tests of particular trends. Before learning, only the linear coefficient was significant for both 5:2 and 5:3. Before learning, participants approximated the intended ratios in a small area around 2:1. After learning and at retention, although most linear and quadratic coefficients were significant, the functions were best captured by the significant higher-order negative cubic terms. For intended ratios of intermediate decimal value [5:3 (1.67) → 3:1 (3.00)], CE was near zero, indicating that the performance of an expanded range of unpracticed ratios approximated the intended ratios. Both 5:2 and 5:3 learners demonstrated positive transfer—increased accuracy of the performance of other ratios—as evidenced by the formation of those negative cubic terms.

We analyzed VE to determine whether improvements in accuracy across the probe ratios were accompanied by improved performance consistency. Fig. 10 depicts frequency ratio VE for the Farey
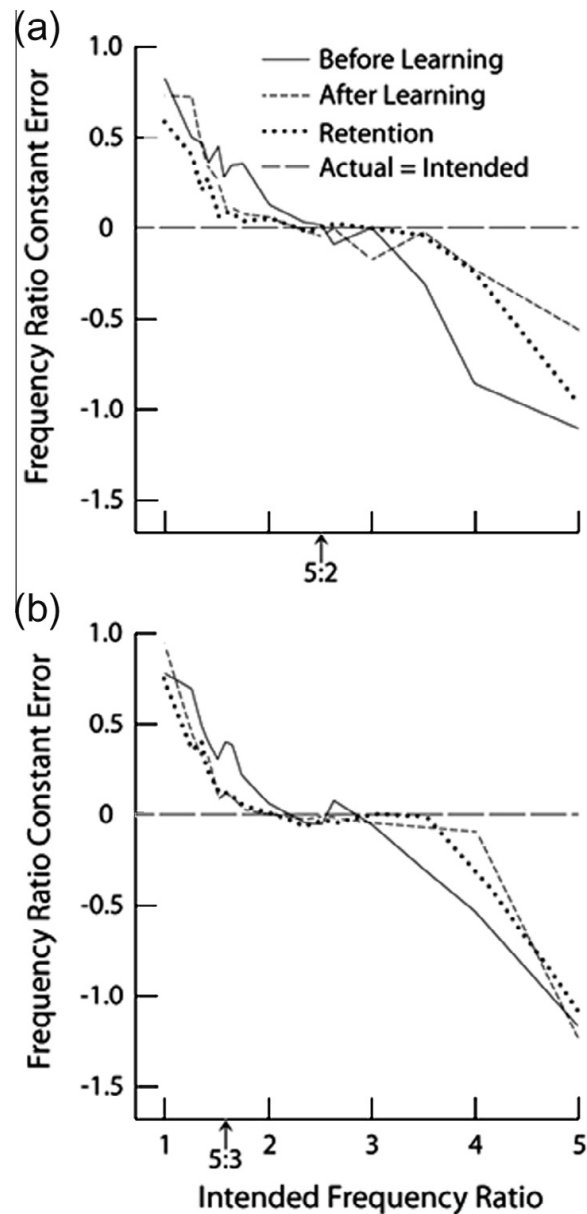
Fig. 9. Frequency ratio constant error in the 5:2 (a) and 5:3 (b) practice conditions as a function of probes (before learning, after learning, and after a one-week retention interval) indicate the formation of a cubic trend after learning. The long dashed line indicates where the performed ratios equal the intended ratios. The practiced ratios (5:2 and 5:3) are marked with arrows.

tree ratios before learning (solid line), after learning (dashed line), and at retention (dotted line) in the 5:2 (Panel A) and 5:3 (Panel B) practice conditions. A 2 (Practice Condition: 5:2, 5:3) × 3 (Probe: before learning, after learning, retention) × 16 (Ratios) ANOVA was performed. The effect of Probe on VE, $F(2,36) = 19.97$, $p < .001$, was significant. Main effect contrasts were performed to compare VE on the different probes. VE was greater before learning than either after learning, $F(1,18) = 22.36$, $p < .001$, or at retention, $F(1,18) = 27.60$, $p < .001$. That pattern of results indicates that learning either 5:2 or 5:3 resulted in the stabilization of most other unpracticed ratios. VE did not differ after learning and at retention, $F(1,18) = 0.23$, $p = .640$. Transfer effects were maintained for at least one week. The effect of Ratio on VE, $F(15,270) = 21.60$, $p < .001$, was also significant. There was a quadratic trend in which ratios of smaller [1:1 (1.00) → 8:5 (1.60)] and larger [7:2 (3.50) → 5:1 (5.00)] decimal value were performed more variably than ratios of intermediate [5:3 (1.67) → 3:1 (3.0)] decimal value. This is expected, given the differences in accuracy observed in Fig. 9. Overall, the results indicated that both 5:2 and 5:3 learners demonstrated positive transfer over an expanded range of unpracticed ratios.

Table 1
Regression analysis of frequency ratio CE as a function of Intended, Intended[2] and Intended[3] ratios in the 5:2 and 5:3 conditions before learning, after learning and at one-week retention.

Probe	R^2	β_1 (Linear)	β_2 (Quadratic)	β_3 (Cubic)	t_1 (Linear)	t_2 (Quadratic)	t_3 (Cubic)	df
5:2								
Before	.52	−.35	.04	−.03	−5.88**	0.58	−1.07	156
After	.47	−.21	.24	−.08	−4.51**	4.24**	−3.71**	156
One-week	.44	−.10	.16	−.09	−1.97	3.09*	−4.03**	140
5:3								
Before	.52	−.34	.10	−.05	−5.71**	1.56	−1.95	172
After	.62	−.11	.29	−.15	−2.35*	6.21**	−7.64**	172
One-week	.48	−.12	.20	−.11	−2.49*	3.97**	−4.89**	172

Note. Analysis performed with centered independent variables.
* $p < .05$.
** $p < .001$.

3.2.1. Relative phase substructure in transfer

We investigated next how those improvements were achieved by examining lagged return plots for all of the probed ratios from the probe trials that occurred after learning. We selected lagged return plots for two ratios to illustrate the general effect. Fig. 11 (top row) depicts lagged return plots for the 7:2 (left panel) and 5:4 (right panel) ratios. Later, we will describe how those two ratios displayed minimal and maximal amounts of chunking, respectively, among all the probed ratios. Once again, the dashed diagonal line in each panel represents the predicted change in relative phase over the time delay if consistent component frequencies were maintained during the entire trial in the performance of that particular ratio. For 7:2 ratio performance, most data were in the vicinity of the dashed diagonal lines. In contrast, for 5:4 ratio performance, data clustered at both 0° and ±180°. This suggests that motor-respiratory performance dwelled in the vicinity of the stable relative phase patterns of inphase and antiphase for some ratios but not for other ratios.

To analyze the relative phase substructure across participants, we calculated the percentage of data points within ±30° of inphase and antiphase from the lagged return plots produced for all participants. Fig. 11 (bottom panel) depicts mean percentages for all the probed ratios from the probe trials that occurred after learning. The data are collapsed across the 5:2 and 5:3 learning conditions. Notice that attraction to the intrinsic relative phase dynamics appears to be greater for ratios closer to 1.0 in which the component frequencies are more similar. The percentage is greatest for the 1:1 ratio, for which participants were expected to perform mostly inphase or antiphase. That should not be considered an indication of chunking. A 2 (Practice Condition: 5:2, 5:3) × 15 (Ratios) ANOVA was performed on the percentages, excluding 1:1 from the analysis. Only the effect of Ratio on the percentages, $F(14, 266) = 21.10$, $p < .001$, was significant.

Following a procedure similar to that used previously to examine the learning trends, we evaluated the percentages for exponential decay across the intended ratios using linear regression. We fit our data to Eq. (3) using regression analyses, where Y was percentage and X was Ratio. To avoid taking logarithms of zero, it was necessary to add 1.0 to each percentage. The following regression equation, excluding data from 4:1 and 5:1 because they did not fall along the same trend as the rest of the data, resulted from the analysis:

$$\log(\text{Percent} + 1) = -0.49\ \text{Ratio} + 1.88. \tag{7}$$

Ratio was a significant predictor of $\log(\text{Percent} + 1)$, $t(271) = 16.08$, $p < .001$, $R^2 = .48$, which indicates that the attraction to the intrinsic relative phase dynamics was greater toward the left side of Fig. 11 (bottom panel), dropped off quickly, and leveled out toward the right side of the figure. Chunking was most apparent for ratios in which the component frequencies were similar (e.g., 5:4). The tendency dropped off as the difference between component frequencies increased and reached the lowest levels when the component frequencies were quite different (around 7:2). However, given that 4:1 and 5:1 did not fall along the same trend, that interpretation may hold best for complex ratios.

4. Discussion

The motor-respiratory coordination literature has focused primarily on documenting the ratios performed (Amazeen et al., 2001; Bramble & Carrier, 1983; Garlando et al., 1985), with only one study on ratio acquisition. Mahler et al. (1991) found that novice rowers could acquire a 1:2 ratio between rowing stroke and breathing frequency over eight months of practice. We extended the results of Mahler et al. by examining the acquisition of more complex ratios that have not been observed widely in the literature (5:2 and 5:3). In contrast to the eight months of practice for Mahler et al.'s participants, we demonstrated that learning of complex ratios could occur over just two days of practice. Participants were able to perform both 5:2 and 5:3 using two markedly different strategies that are discussed below.

Different learning timelines in Mahler et al. (1991) and the current study could be the result of different constraints on coordination. There are strong mechanical constraints on rowing, such as compression of the lungs that occurs during each forward reach (Cunningham, Goode, & Critz, 1975). Such
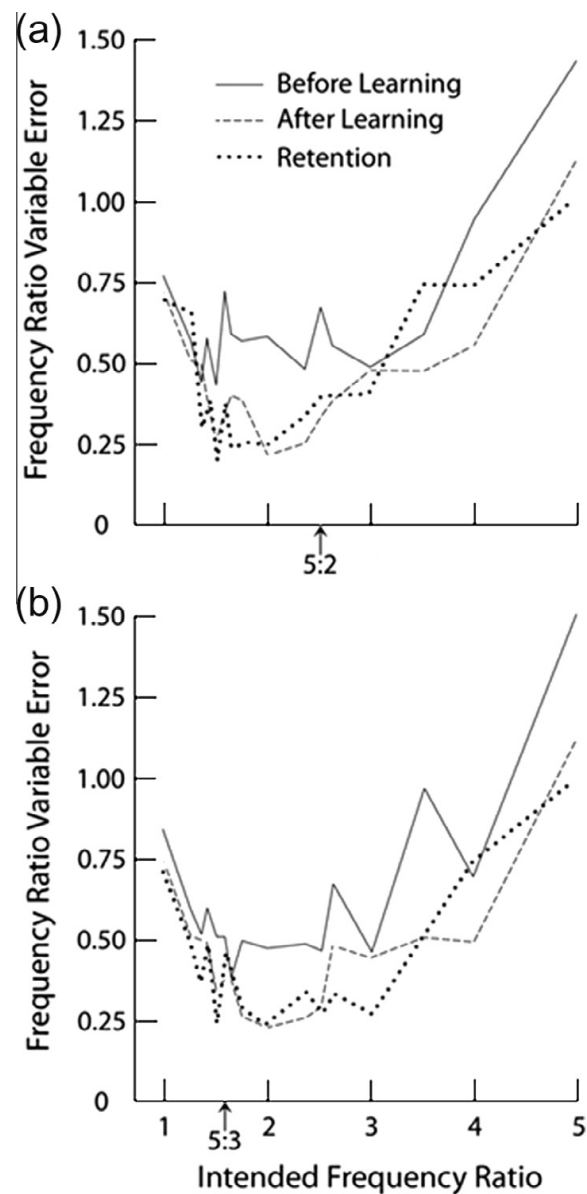

Fig. 10. Frequency ratio variable error in the 5:2 (a) and 5:3 (b) practice conditions as a function of probes (before learning, after learning, and after a one-week retention interval) indicate a drop in variability across the majority of ratios after learning. The practiced ratios (5:2 and 5:3) are marked with arrows.
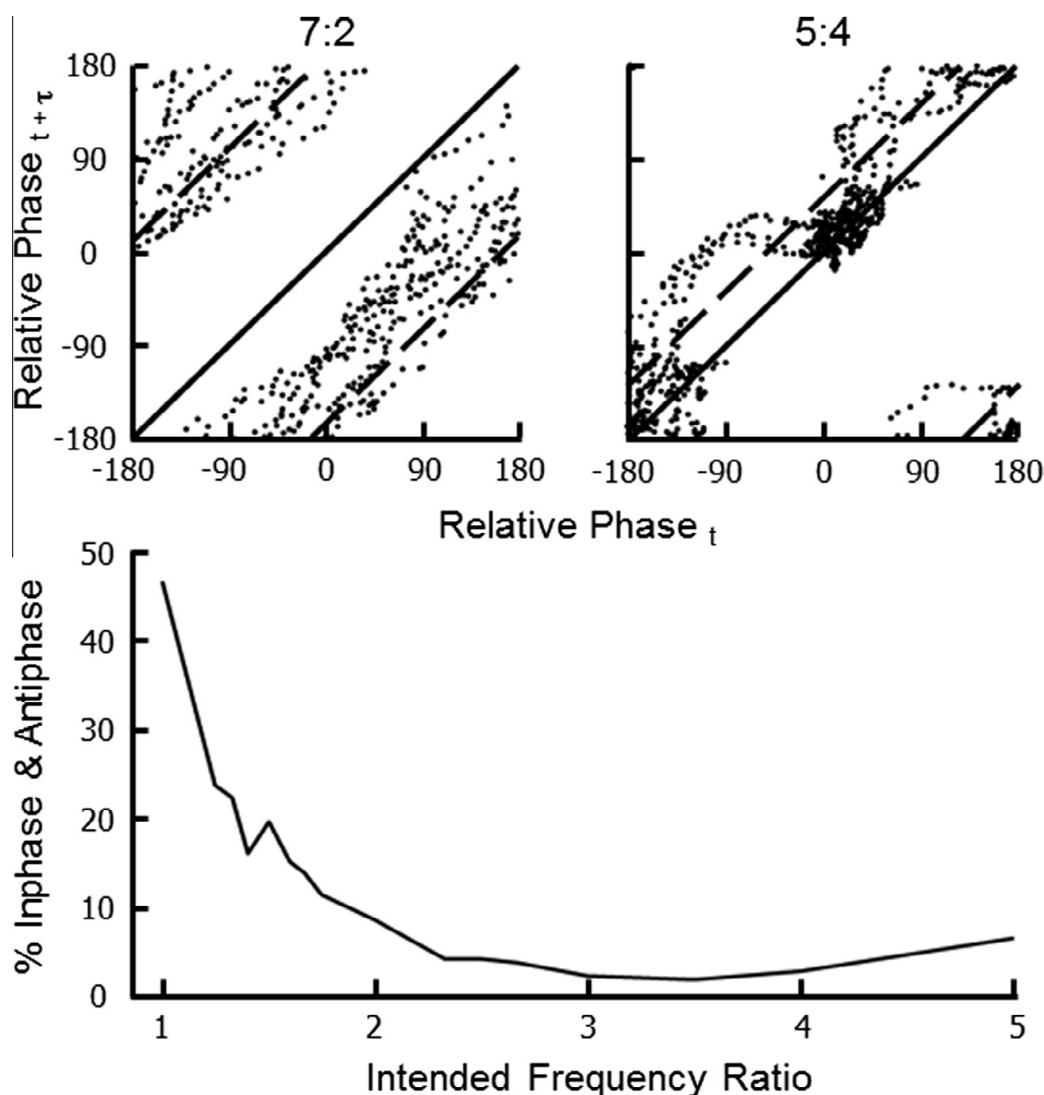
Fig. 11. Lagged return plots from the after-learning probe (top row) depict the evolution of relative phase over a time delay (τ) for representative participants performing 7:2 (left panel) and 5:4 (right panel). The percentage of points around inphase and antiphase (bottom panel) as a function of the intended ratio for all participants.

constraints could limit the range of frequency ratios that are possible with the rowing stroke, making motor-respiratory coordination more difficult in rowing than in the arm movement task of the current study. Another possible explanation for the faster learning timeline in the current study is that the performance templates, which present simple information about the relative timing of movement and breathing landmarks could facilitate both learning and transfer. In support of that explanation, Hessler et al. (2010) found that ratio performance was more accurate with the performance template in comparison to a "no display" control condition.

4.1. Differences in ratio learning

We used the sine circle map, a dynamical model of two-frequency resonances, to make predictions about the stability of multifrequency performance in motor-respiratory coordination. That model has been used previously in both the motor coordination literature (e.g., de Guzman & Kelso, 1991; Gonzales et al., 2010; Hessler et al., 2010; Peper et al., 1991, 1995a,b; Treffner & Turvey, 1993) and in other fields in which multifrequency patterns are observed (e.g., Glazier & Libchaber, 1988). Predictions of the sine circle map are captured in a mathematical structure called the Farey tree. The two ratios that we focused on in the present study reside on the same level of the Farey tree.

The implication is that they should be equivalent in terms of performance stability. However, 5:3 performance involves more complex relative phase relations than 5:2 performance. It is that latter distinction that allows for the prediction of differential stability.

Observations from various interlimb coordination studies, in which 5:3 performance was less stable than 5:2 performance, support that prediction (Peper et al., 1991; Summers, Rosenbaum, Burns, & Ford, 1993; Treffner & Turvey, 1993). All of those studies used mean performance (accuracy and stability) to compare ratio performance. Summers, Rosenbaum, et al. also provided more detailed timing information such as deviations from expected intervals in a tapping task. In examining mean accuracy and stability, we saw no notable differences between 5:3 and 5:2. Performance of 5:3 and 5:2 improved to a similar degree with practice, and learning effects were retained after one week. The result that acquisition of 5:3 and 5:2 was equivalent is seemingly inconsistent with previous results in interlimb coordination. It was only when we examined histograms of ratio performance (Fig. 7) and the time evolution of relative phase trajectories using lagged return plots (Fig. 8) that we observed differences. The 5:2 ratio was performed using *more accurate* frequency and relative phase relations, whereas the 5:3 ratio was performed using *more stable* frequency and relative phase relations.

Returning to the Farey tree, we note that ratios from higher levels of the Farey tree are predicted to be less stable than ratios that reside at lower levels of the tree (Glass & Mackey, 1988; González & Piro, 1985; Jensen et al., 1984; Schroeder, 1991). Previous studies on both motor-respiratory coordination during bicycling (Villard et al., 2005) and interlimb coordination (de Guzman & Kelso, 1991; Haken et al., 1996; Peper et al., 1991, 1995a,b; Treffner & Turvey, 1993) have reported transitions from higher-level toward lower-level ratios in support of that prediction. In the current study, histograms of per-cycle performance revealed that the 5:2 ratio was performed both accurately and stably. In contrast, when participants attempted the more difficult 5:3 ratio, learners combined 3:2 and 2:1—both lower-level ratios along the same branch of the Farey tree as 5:3—to produce the overall pattern. Similar chunking behavior is likely to occur in other exercises like bicycling in which transitions to lower-level ratios have been observed. One consequence of this so-called chunking was an improvement in the mean performance of 5:3. Another consequence was the performance, intentional or unintentional, of the stable relative phase patterns of inphase and antiphase. We turn to the significance of those two patterns with respect to performance stability in the context of the interlimb coordination literature.

4.2. Naturally stable patterns influence learning

We examined the extensive literature on learning in interlimb coordination to help inform the study of learning in motor-respiratory coordination. The first important finding from interlimb coordination was that naturally stable coordination patterns can influence the acquisition of novel coordination patterns (Kostrubiec et al., 2006, 2012; Zanone & Kelso, 1992a,b; Zanone et al., 2010). During learning, more stable coordination patterns can provide a stable position from which to anchor acquisition. For example, in interlimb coordination, participants with a bistable repertoire (inphase and antiphase) approximated the gallop pattern from the direction of antiphase (Zanone & Kelso, 1992a) and participants with a multistable repertoire (inphase, gallop, and antiphase) temporarily shifted the location of the gallop pattern attractor in the direction of 135° relative phase (Kostrubiec et al., 2006). However, attraction to very stable patterns may be detrimental to learning because performance can become locked onto those patterns; Zanone and Kelso (1992a) explain that inphase may not be a good starting point for the performance of other relative phase patterns for that reason.

In the present study, participants were attracted to both more stable frequency ratios and more stable relative phase patterns of inphase and antiphase. By definition, performance of multifrequency ratios entails traversing all relative phase patterns; maintenance of a single relative phase relation would result in monofrequency performance. For idealized multifrequency ratio performance, in which the correct component frequencies (for the intended ratio) are maintained during an entire trial, relative phase drift is constant. To examine the relative phase dynamics, we used a novel analytical technique called lagged return plots, a plot of relative phase values at time t against relative phase values after a time delay $t + \tau$. Lagged return plots were useful in exploring the finer temporal structure within frequency ratio performance. For performance of 5:3, there was a clear preference for

maintaining inphase and antiphase across the time delay (Fig. 8). Those results, which are consistent with the preference for and greater stability of inphase and antiphase in interlimb coordination (Haken et al., 1985; Kelso, 1984) and coordination between wrist pronation-supination and breathing (Temprado et al., 2002), are preliminary evidence for the significance of component relative phase patterns in motor-respiratory coordination. The fact that inphase and antiphase were preferred during motor-respiratory coordination tasks in which mechanical and energetic constraints were weak holds promise for similar findings in exercises in which the mechanical and energetic constraints on motor-respiratory coordination are stronger.

Phase attraction, defined as the tendency to perform particular relative phase patterns over others, has also been observed previously in multifrequency interlimb coordination (de Guzman & Kelso, 1991; Summers, Ford, & Todd, 1993; Summers & Kennedy, 1992; Summers, Rosenbaum et al., 1993). In de Guzman and Kelso (1991), participants coordinated movement of the index fingers, with one finger moved actively and the other finger driven by a torque motor. During the performance of 2:1, there was phase attraction to inphase and antiphase, followed by brief transitions between those patterns. Based on that result, they proposed a modified version of the sine circle map with built-in phase attraction, referred to as the phase-attractive circle map. In the studies by Summers and colleagues, musicians and nonmusicians tapped out frequency ratios between the index fingers (5:3 in Summers, Ford et al., 1993 and Summers & Kennedy, 1992; 5:4, 4:3, 3:2, 5:3, and 5:2 in Summers, Rosenbaum et al., 1993). Participants produced the correct timing relations for the 3:2 and 5:2 ratios. Sometimes, taps shifted toward inaccurate antiphase relations for the 5:4, 4:3, and 5:3 ratios, especially among nonmusicians. More accurate relative phase patterning for 5:2 than 5:3 is consistent with the findings of the current study. Together with those previous findings, our findings support the convergence of literature on relative phase and multifrequency coordination.

4.3. Transfer to unpracticed patterns

The second important finding from learning in interlimb coordination was that practice of one coordination pattern can result in transfer to other, unpracticed coordination patterns (Fontaine et al., 1997; Lee et al., 1995; Zanone & Kelso, 1992a,b, 1997). Following acquisition, we observed positive transfer that was consistent across both the 5:2 and 5:3 practice conditions. Accuracy improved across a large range of ratios (5:3 to 3:1) and stability increased across nearly the entire range of ratios. Although learners performed 5:2 consistently and combined more stable chunks of rhythmic behavior to produce the overall 5:3 pattern, those differences did not influence transfer. How participants realized transfer improvements depended on the similarity of the component frequencies for each frequency ratio. We again examined ratio performance using lagged return plots. Relative phase relations are traversed more quickly when the component frequencies are more different, leaving less time to dwell at the intrinsically stable states of inphase and antiphase. Thus, it was not surprising that the change in relative phase over a time delay was more consistent for ratios whose component frequencies differed substantially. In contrast, participants dwelled more at inphase and antiphase when performing ratios whose component frequencies were more similar. Participants combined more stable chunks of rhythmic behavior in their performance of those ratios.

In the introduction, we indicated that the specificity of transfer in the learning of multifrequency ratios was still open to empirical inquiry. The positive transfer effects observed in the current study were not highly specific to the ratios learned nor did they generalize to all tested ratios. Participants did not simply gain more refined control over the practiced frequency relations (W in the sine circle map) through the learning process. If they had, then increases in the accuracy and stability of the performance of other ratios along the same branch of the Farey tree would be expected (Haken et al., 1996). Training also did not facilitate communication broadly across the physiological subsystems of the body (K in the sine circle map). If it had, then increases in the accuracy and stability of all ratios would be expected (Jagacinski et al., 2000). The question then turns to how we might account for the observed positive transfer effects. The preliminary answer is to use the type of model proposed by Jagacinski et al. (2000) in which there are multiple coupling terms, each of which encompasses several ratios. Positive transfer predictions from such a model would be more general than models with ratio-specific coupling terms (Haken et al., 1996) but more specific than models with a single coupling

term like the sine circle map. How the multiple coupling terms should be defined is still unclear and requires examination of the learning process for additional ratios beyond the two tested here.

4.4. Limitations and future directions

One surprise in the transfer results that contradicts both predictions regarding ratio performance and previous findings in the literature was the finding that complex ratios, like 7:4 and 8:3, were performed more accurately than simple ratios, like 1:1 and 5:1. In the current study, we held movement frequency constant to maintain control over coupling strength, which is known to be related to movement frequency. With movement frequency constrained, the required breathing frequency needed to perform particular ratios was sometimes much faster (0.67 Hz for 1:1) or slower (0.13 Hz for 5:1) than the preferred breathing frequency. The negative slopes in Fig. 9 are consistent with that explanation. For ratios of smaller decimal value (e.g., 1:1), participants underestimated the breathing frequency, producing a positive constant error. Likewise, for ratios of larger decimal value (e.g., 5:1), participants overestimated the breathing frequency, producing a negative constant error. If frequency constraints were loosened in future experiments, then we would expect both movement and breathing frequency (and, also, coupling strength) to vary more freely across ratios, and ratios like 1:1 and 5:1 to be performed more accurately and consistently.

There is a natural connection between research on motor-respiratory coordination and application to sport. A common observation in the literature is the modulation of performed frequency ratios, from one intrinsically stable ratio to another, in response to changing athletic demands (e.g., Amazeen et al., 2001; Bramble & Carrier, 1983; Garlando et al., 1985). Our results indicate that participants are able to stabilize more ratios, especially complex ratios, than were reported previously in the literature. Our choice of a simple arm movement task likely facilitated the performance of ratios that might pose hazards during activities like running, in which the legs must support the body as well as synchronize with breathing in the prescribed manner. We therefore expect the ratios that may be performed during sport are likely to be more limited than they were in the present study. However, we believe that there are useful applications of our findings to sport.

An expanded repertoire of ratios may allow for greater flexibility during exercise, both for athletes and non-athletes. That possibility could be explored by examining both the ratios used and the corresponding efficiency of performance over variations in movement frequency. We recognize, however, that there still exists a natural limitation on ratio performance. In the current study, participants harnessed the intrinsic stability of other frequency and relative phase relations in performing ratios in motor-respiratory coordination. In future studies, we could leverage that chunking strategy and potentially increase flexibility by training athletes to become more proficient at switching between stable coordination patterns. That is, instead of trying to train participants to perform 5:3, they could be trained explicitly to switch between ratios like 3:2 and 2:1. The result could be smoother modulation of the ratios used, and perhaps greater exercise efficiency, in response to changing athletic demand.

5. Conclusion

Although the particular bodily subsystems involved differ, the findings that we observed for motor-respiratory coordination in the present study are, in many ways, similar to the patterns of learning and performance that are observed in interlimb coordination. The sine circle map is useful in the determination of transition pathways and/or ratio stability in both motor-respiratory and interlimb (Peper et al., 1995a,b; Treffner & Turvey, 1993) coordination. Moreover, the finding of the current study, that inherent in the performance of multifrequency ratios is an attraction to the commonly observed and stable inphase and antiphase patterns, is consistent with previous observations in the interlimb literature (de Guzman & Kelso, 1991; Summers, Ford et al., 1993; Summers & Kennedy, 1992; Summers, Rosenbaum et al., 1993). Theoretically, motor-respiratory and interlimb coordination may share common dynamical properties that operate both between and within bodily subsystems. The extent to which we observe similarities among coordination phenomena (e.g., motor-respiratory, interlimb,

neural, social) is evidence for generalized coordination tendencies (Kelso, 1995). Thus, it might be fruitful, as it was in this study, to examine well-understood coordination phenomena for potential insights about less-researched coordination phenomena.

Acknowledgements

Appendix A

Given the 25 Hz sampling rate used in the current study, the temporal resolution for the collection of movement and breathing data was 0.04 s. Measurements need to be precise to differentiate between neighboring frequency ratios. We calculated confidence intervals around each frequency ratio to characterize measurement error based on the 25 Hz sampling rate. Those confidence intervals, represented as distributions around each frequency ratio value, are presented in Fig. A1. Below, we describe the calculation of those distributions and how those distributions relate to the ability to differentiate between neighboring frequency ratios.

Although the temporal resolution was the same for movement and breathing, the length of the movement and breathing cycles differed according to the required frequency ratio. We calculated the minimum and maximum cycle lengths for each required movement and breathing frequency. For example, for a required frequency ratio of 5:4, the average length of the movement cycle was 1.49 s (±0.04 = 1.45 to 1.53 s) and the average length of the breathing cycle was 1.87 s (±0.04 = 1.83 to 1.91 s). Using those minimum and maximum cycle lengths, we determined the temporal resolution for the calculation of each ratio based on the 25 Hz sampling rate. For 5:4 (1.25), the calculated ratio could vary between 1.19 and 1.31. The confidence interval for 5:4 was 1.25 ± 0.06 s.

The size of the confidence intervals varied across the required frequency ratios, with a minimum of ±0.05 for the 1:1 ratio and a maximum of ±0.16 for the 5:1 ratio. We expect each confidence interval to follow a normal distribution, with small deviations from the required frequency ratio more likely to occur than large deviations (the extreme case in which movement period is grossly overestimated and breathing period is grossly underestimated or vice versa). Those confidence intervals are depicted as distributions in Fig. A1.

When distributions overlap, there is potential for one ratio to be confused for another in the ratio calculations. The pairs of distributions that overlap were: 5:4 and 4:3; 4:3 and 7:5; 7:5 and 3:2; 3:2 and 8:5; 8:5 and 5:3; 5:3 and 7:4; 7:3 and 5:2; 5:2 and 8:3. In most of those cases (5:4 and 4:3; 4:3 and 7:5; 7:5 and 3:2; 3:2 and 8:5; 5:3 and 7:4; 7:3 and 5:2; 5:2 and 8:3), the overlap is small, occurring in the tails of the distributions. The probability associated with overlap in the tails is extremely small, requiring large deviations from the two neighboring ratios in opposite directions. The scenario is made less likely by our use of cycle-by-cycle calculations of the frequency ratio: over the course of a trial, small deviations based on sampling rate error are likely to average to a value closer to the center of each distribution.
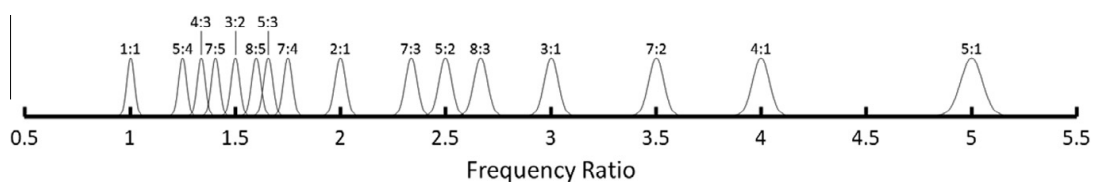

Fig. A1. Confidence intervals represented as distributions around each frequency ratio value characterize measurement error based on a 25 Hz sampling rate.

As identified in the text, two ratios overlap sufficiently so as to cause potential concern: 8:5 and 5:3. The upper tail of the 8:5 distribution reaches the mean for the 5:3 distribution (1.67), and the lower tail of the 5:3 distribution reaches the mean for the 8:5 distribution (1.60). The probability that an estimation error would occur depends on (a) large deviation from one of the required frequency ratios rather than from both, as outlined above for the seven other ratio pairs; or (b) medium deviation in opposite directions from both required ratios.

The conclusion that we draw is that the impact of sampling rate on ratio confusion varies according to the ratio pair being considered. The vast majority ($n = 52$) of ratio pairs (e.g., 5:1 and all other ratios) are unaffected by the 25 Hz sampling rate. Ratio confusion for seven ratio pairs is possible but improbable. The greatest possibility for ratio confusion is between 8:5 and 5:3. In that case, estimates of the onset of each movement and breathing cycle could deviate in opposite directions with sufficient regularity so as to shift the estimate of the mean performed frequency ratio over the course of the trial. If that occurs in opposite directions (an overestimate for 8:5 and an underestimate for 5:3), then performance of 8:5 could be misinterpreted as actual performance of 5:3 or vice versa.

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