Journal of Experimental Psychology:
Human Perception and Performance
2001, Vol. 27, No. 5, 1243–1259

0096-1523/01/$5.00 DOI: 10.1037//0096-1523.27.5.1243

Coupling of Breathing and Movement During Manual Wheelchair Propulsion

Polemnia G. Amazeen, Eric L. Amazeen, and Peter J. Beek
Vrije Universiteit, Amsterdam

The hypothesis of this study was that stable coordination patterns may be found both within and between physiological subsystems. Many studies have been conducted on both monofrequency and multifrequency coordination, with a focus on both the frequency and phase relations among the limbs. In the present study, locomotor–respiratory coupling was observed in the maintenance of small-integer frequency ratios (2:1, 3:1, and 4:1) and in the consistent placement of the inspiratory phase just after the onset of the movement cycle during wheelchair propulsion. Level of experience and various motor and respiratory parameters were manipulated. Coupling was observed across levels of experience. Increases in movement frequency were accompanied by a shift to larger-integer ratios, suggesting that a single modeling strategy (e.g., the Farey tree; D. L. González & O. Piro, 1985) may be used for coordination both within the motor subsystem and between it and other physiological subsystems.

Humans and animals alike demonstrate a discrete number of stable coordination patterns. Patterns of locomotion, called *gaits*, are limited in number and easily recognizable. For quadrupeds, the three most common gaits are the walk, trot, and gallop, although more complex subdivisions of gait are possible (for an overview, see Collins & Stewart, 1993; Schöner, Jiang, & Kelso, 1990). In bipedal locomotion, spontaneously produced patterns are limited to the walk or run (antiphase) and the jump (inphase) patterns. In all of these patterns, the limbs move at the same frequency, so that the different patterns may be characterized by different phase relations between the limbs. When the constraint of postural stability is removed, observed motor patterns become more complex and different phase relations (e.g., 90°, Zanone & Kelso, 1992, 1997) can be acquired. The HKB model, a dynamical model first developed by Haken, Kelso, and Bunz (1985), accommodates the different monofrequency coordination patterns observed including the effects of learning, handedness, and attention (see summary in Amazeen, Amazeen, & Turvey, 1998). Multifrequency coordination patterns—in which the limbs move at different frequencies, as in drumming (e.g., Peper, Beek, & van Wieringen, 1995a, 1995b), and may be spontaneously produced or learned—are also accommodated by an expansion of the HKB model (Sternad, Turvey, & Saltzman, 1999a, 1999b) or by other mathematical structures like the Farey tree (e.g., González & Piro, 1985). In all of the aforementioned patterns, coordination takes place between two or more limbs or limb segments, that is, within a motor subsystem. The present study was designed to explore the possibility that coordination may take place between physiological subsystems. The presence of intermodal coupling would suggest that coordination is a basic phenomenon that may be observed whenever two or more rhythmic processes interact. The phenomenon we focused on was *locomotor–respiratory coupling* (LRC), the pacing of breathing while exercising. If LRC is observed, then the observed patterns may indicate some common basis for modeling.

Polemnia G. Amazeen, Eric L. Amazeen, and Peter J. Beek, Faculty of Human Movement Sciences, Vrije Universiteit, Amsterdam, the Netherlands.

Eric L. Amazeen is now at the Department of Psychology, Arizona State University.

Preliminary findings were reported in Amazeen, Amazeen, and Beek (1999). Support was provided by Vrije Universiteit Grant USF'96 awarded to Peter J. Beek.

We would like to acknowledge the assistance of Luc van der Woude, Annet Dallmeijer, Jos van den Berg, and Bert Clairbois in the preparation of the experiments and the assistance of Jay Holden in the comparison of left and right limb movements.

Correspondence concerning this article should be addressed to Polemnia G. Amazeen, who is now at the Department of Psychology, Arizona State University, P.O. Box 871104, Tempe, Arizona 85287-1104. Electronic mail may be sent to nia@asu.edu.

Locomotor–Respiratory Coupling

Coupling may be operationalized as either the consistent phasing (e.g., inphase) or maintenance of a small-integer frequency relation (e.g., 2:1) of two rhythmic processes. In this sense, the term applies to coordination within the motor subsystem, where the focus is on phasing during monofrequency coordination and on frequency ratios during multifrequency coordination. Because the movements of a limb or limb segment are usually faster than respiration, LRC is comparable to multifrequency coordination; therefore, the literature focuses predominantly (but not exclusively) on identifying the frequency ratios that are used. LRC has been observed during both quadrupedal and bipedal locomotion. LRC was first studied in a young jackrabbit that was trained to run on a treadmill (see Bramble & Carrier, 1983). At low speeds, it completed two full breathing cycles per locomotory cycle. At higher speeds, it switched to a 1:1 (monofrequency) ratio between stride frequency and respiratory frequency. The components of LRC were studied more extensively in another quadruped, the horse, which maintains a constant 1:1 ratio during the canter (slow gallop) and gallop (Bramble & Carrier, 1983; Lafortuna, Reinach, & Saibene, 1996). Human runners demonstrate more flexibility than quadrupeds, shifting from 4:1 (four strides per breath) to 2:1 with increased velocity and altering frequency ratios (e.g., 2:1, 3:1, 4:1, 3:2, 5:2) during steady-state behavior (Bramble & Carrier, 1983).

Phase analyses that have been conducted on human runners reveal a preference for initiating and terminating a respiratory cycle with either the left or right foot during level track running when even ratios (e.g., 2:1, 4:1) are used (Bramble & Carrier, 1983). Phase relations differ for uphill and downhill running; inspiration was observed during the support phase of the step in uphill running and during the swing phase of the step in downhill running (Takano, 1995). No consistent phasing was observed in relation to the onset of expiration, which suggests that inspiration is more closely coupled to motor processes than is expiration. Individual differences—that is, consistency of phasing strategy within an individual but not between individuals—have been documented as well (Bernasconi & Kohl, 1993), although the development of those individual strategies has not been studied.

When Is LRC Observed?

A large number of studies have been conducted on LRC during human lower-limb locomotion, like running and bicycling. Untrained bicyclists have been shown to maintain a 2:1, 3:1, 4:1, 6:1, 3:2, and 5:2 ratio of pedal to respiratory frequency (Garlando, Kohl, Koller, & Pietsch, 1985; Paterson, Wood, Morton, & Henstridge, 1986). The variability of ratios observed may indicate that LRC is more stable in some activities than in others. A direct comparison of running and cycling revealed a greater degree of coupling, as defined by phase, during running (Bernasconi & Kohl, 1993). In general, experienced runners and cyclists have been shown to have a higher degree of coupling than untrained individuals (Bramble & Carrier, 1983; Kohl, Koller, & Jäger, 1981), although no systematic study of LRC changes during training in these sports has been conducted.

Although it is tempting to believe that LRC only occurs when both frequency and phase coupling are observed, an absence of frequency and/or phase locking does not necessarily imply that coupling is absent. According to the theory of coupled oscillators, coupling between two rhythmic processes may be too weak to induce both frequency and phase locking. Evidence of weaker coupling takes the form of relative coordination, in which the component processes pass into and out of a coordinated state rather than maintain coordination steadily (von Holst, 1939). Relative coordination may be practically observed as bouts of coupling and decoupling or as switching among frequency ratios and/or phase relations. Although it is tempting to think of weak coupling as synonymous with inexperience, a notable observation is the intentional use of relative coordination by competitive cyclists, who report that the intentional decoupling of locomotion and respiration allows them to shift gear ratios more easily (Garlando et al., 1985). The uncoupled state cannot be maintained because oxygen consumption is least—and therefore exercise is most efficient—during LRC (Bernasconi & Kohl, 1993; Garlando et al., 1985). Therefore, experience may not provide for stronger coupling but rather for greater control over the presence or absence of coupling.

A number of studies have looked for a coupling mechanism to derive a rule for the presence or absence of coupling. The seemingly greater efficiency of coupling over noncoupling seems to imply a bidirectional influence, and yet LRC is largely assumed to be unidirectional, from the motor subsystem to the respiratory subsystem, rather than vice versa (Astrand & Rodahl, 1977; Bechbache & Duffin, 1977; Bramble & Carrier, 1983; Kao, 1963; Paterson et al., 1986). One of the most widely accepted mechanisms for LRC has been the *visceral piston,* a metaphor for the rhythmic perturbation of the diaphragm by any vertical impulse (Bramble & Carrier, 1983; Bramble & Jenkins, 1993; Paterson et al., 1986). This model assigns causal priority to the motor subsystem rather than to respiration. During running, vertical impulses are generated by the ground reaction force of footfalls, producing the coupling that is observed between movements and respiration. In contrast, any activity that involves only the upper limbs does not generate a vertical impulse and so, according to the visceral piston hypothesis, should not produce LRC.

Evidence from the literature on upper-limb locomotion suggests otherwise. LRC has been observed in bats and various species of flying birds (e.g., Butler & Woakes, 1980; Suthers, Thomas, & Suthers, 1972) and in the human activity of rowing (Mahler, Hunter, Lentine, & Ward, 1991; Mahler, Shuhart, Brew, & Stukel, 1991). In one study, elite rowers demonstrated frequency ratios of 1:1 and 1:2 (rowing strokes per breath) and inspired at phases of the rowing cycle that were consistent within each rower but differed across rowers (Mahler, Shuhart, et al., 1991), suggesting different LRC strategies. In another study, novices produced the 1:2 ratio only during submaximal exercise intensities (Mahler, Hunter, et al., 1991). Following training, they became much more consistent, maintaining a 1:2 ratio during both submaximal and peak exercise and developing a phasing strategy in which they inspired just after the beginning and end of each rowing stroke. The lack of a vertical impulse in rowing implies that the visceral piston is not solely responsible for producing LRC. Rather, LRC may be observed whenever there is a simple mechanical interaction between the motor and respiratory subsystems. The evidence from the motor coordination literature—particularly the finding that the HKB model holds for coordination both within a single individual and between individuals (e.g., Amazeen, Schmidt, & Turvey, 1995; Schmidt, Carello, & Turvey, 1990)—suggests that some form of interaction between two systems is all that is required for stable coordination to occur.

Although rowing is not a prototypical form of locomotion, wheelchair propulsion is for many disabled populations. This leads to a number of practical reasons for its study, including the development of efficient rehabilitation strategies for wheelchair users. In the only study to date on LRC during manual wheelchair propulsion, wheelchair basketball players were asked to propel a wheelchair on a treadmill with a 3% slope at speeds below, at, and above their previously established comfortable wheelchair speeds (MacDonald, Kirby, Nugent, & MacLeod, 1992). A frequency-based definition of LRC was used in which coupling was defined as the coincidence of characteristic frequencies from the power spectra of the propulsion and respiratory time series. A frequency ratio of 3:1 was witnessed on 40% of the trials, although breath-by-breath analyses revealed that the coupling ratio for each breath alternated among 2:1, 3:1, and 4:1 patterns. Both propelling and respiratory frequency increased as a function of velocity, but the ratio of the two was indifferent to the velocity manipulation. A control analysis was performed by calculating the ratios across the propulsion and respiratory frequencies of different participants. MacDonald et al. (1992) concluded that LRC had not actually occurred because the incidence of "false" coupling was 27%. They attributed the absence of LRC during wheelchair propulsion to the exclusion of the abdominal visceral piston. However, given that LRC occurs during rowing (Mahler, Hunter, et al., 1991; Mahler, Shuhart, et al., 1991), it is equally plausible that the methodological constraints of MacDonald et al.'s experiment precluded the observation of LRC during manual wheelchair propulsion.

Goals of the Present Study

The present set of experiments was designed to reconsider the occurrence of LRC during manual wheelchair propulsion. LRC clearly occurs during lower-limb activities like running and bicycling. Observations of frequency and phase coupling during upper-limb locomotion will strengthen the argument that coordination is a general phenomenon that occurs both between and within bodily subsystems. Three experiments were conducted that addressed (a) the existence of coupling during upper-limb locomotion, (b) relevant parameters that cause changes in frequency ratios, and (c) the directionality of the coupling. If patterns of LRC mimicked the results of other tasks limited to interlimb coordination, then we expected that a common basis for modeling could be discovered. The precise form of the modeling would depend on the particular pattern of results that is observed.

To improve the likelihood of observing LRC, we made a number of methodological alterations to the MacDonald et al. (1992) study. First, we tested able-bodied participants, so that we were able to avoid the influence on LRC of potential respiratory and/or motor problems that are associated with spinal cord injuries or that may have resulted from secondary medical complications associated with wheelchair use (Glaser, Sawka, Young, & Suryaprasad, 1980; Janssen, van Oers, Hollander, Veeger, & van der Woude, 1993). Nonwheelchair-dependent populations also tend to be more homogeneous and can be challenged to a greater degree during wheelchair exercises (van der Woude, van Croonenborg, Wolff, Dallmeijer, & Hollander, 1999). Challenge may be operationalized as the participant's energy expenditure or power output, which is the product of velocity and any resistance (e.g., air and friction) that the participant encounters during the task. MacDonald et al. (1992) tested the impact of velocity only on LRC, but other experiments on wheelchair propulsion have varied the rolling resistance of the wheels to control for resistance and, therefore, to influence power output (e.g., van der Woude et al., 1988). Therefore, a second alteration to MacDonald et al.'s methodology that we introduced was the manipulation of both velocity and rolling resistance in Experiment 1, to determine both their individual effects and their joint influence (through power output) on LRC. Movement frequency was manipulated in Experiment 2 to provide for comparisons of observed frequency ratios with the multifrequency coordination literature.

Two alterations were made to the analyses that were performed by MacDonald et al. (1992). First, because participants are likely to alter their propulsion and/or respiratory patterns during the course of a trial, cycle-by-cycle analyses of frequency ratio were performed instead of using summary values. A control analysis of the kind performed by MacDonald et al. was not used because individual participants with similar physical abilities are likely to elect the same characteristic frequency of propulsion for similar task constraints. For example, in the present study, 2 male participants elected a propulsion frequency of 0.97 Hz when asked to propel the wheelchair ergometer at 3 km/hr. Even if their respiratory frequencies differed to produce a conclusion of LRC within each individual (e.g., 0.32 Hz for Participant A yields a ratio of 3:1, and 0.24 Hz for Participant B yields a ratio of 4:1), calculating the ratios across participants (yielding 4:1 and 3:1) would have negated the LRC conclusion. Second, both frequency and phasing analyses were performed to determine the degree, and possibly the directionality, of the coupling. A conclusion of coupling—as indexed by the occurrence of frequency and/or phase locking—would reinforce the notion of a necessary coordination of the motor and respiratory subsystems during upper-limb activity.

Experiment 1: Demonstration of LRC

The first experiment was simply directed at the demonstration of LRC during manual wheelchair propulsion. Able-bodied participants were tested to eliminate the possible confounding influence of respiratory and/or motor dysfunction on coupling. If LRC occurs, then it is possible that able-bodied wheelchair users, like runners, may alter their frequency ratios as a function of velocity. A unique aspect of wheelchair propulsion is that power output may be manipulated by varying both velocity and the rolling resistance of the wheels. Both manipulations were performed in the present experiment to determine whether frequency ratios and/or phasing would change as a function of the relative challenge of wheelchair propulsion to the motor subsystem.

Method

Participants. Seven able-bodied participants (5 men, 7 women; 25–44 years old; all right-handed) volunteered to participate in the experiment. Their wheelchair experience ranged from never having propelled a wheelchair ($n = 5$) to having participated in and conducted wheelchair experiments for 5 ($n = 1$) to 15 ($n = 1$) years. Participants were asked to refrain from smoking and from ingesting caffeine and/or alcohol for at least 2 hr prior to testing. They were asked to eat a light meal 2 hr before the experiment. All participants were naive to the purpose of the experiment. To retain the experience level of each of the participants, we did not permit any of the participants to practice with the equipment prior to the experiment.

Apparatus. The experiment was run on a stationary wheelchair ergometer (Figure 1), whose physical dimensions and rolling characteristics could be altered to accommodate the anatomical dimensions and physical abilities of the individual participant (Neising et al., 1990). Individual adjustment of the seat height and width was required to maximize the efficiency of wheelchair propulsion. Following experimental protocol of past studies (e.g., van der Woude et al., 1999; Veeger, Lute, Roeleveld, & van der Woude, 1992), we adjusted the seat height until the participant's elbow angles were 110° (with 180° defined as full extension), and we adjusted the seat width until either the participant's shoulders were located directly over the wheel rims or, if the shoulders were not wide enough, the sides of the wheelchair seat rested against the participant's hips. The seat position was recorded and maintained during the course of the experiment. A monitor that was placed at eye height in front of the participant displayed both the required and actual velocity of the wheels. Propulsion frequency was indexed as the rate of torque application to the right wheel rim,[1] which was measured directly from the ergometer at 100 Hz.

An air flow measurement system, or pneumotachometer (Hans Rudolph, Inc., Kansas City, MO) was used to measure respiratory frequency by means of the differential pressure method. Two membranes that were

[1] The correlation between the right and left wheel rim exceeded .90 for all dependent measures.

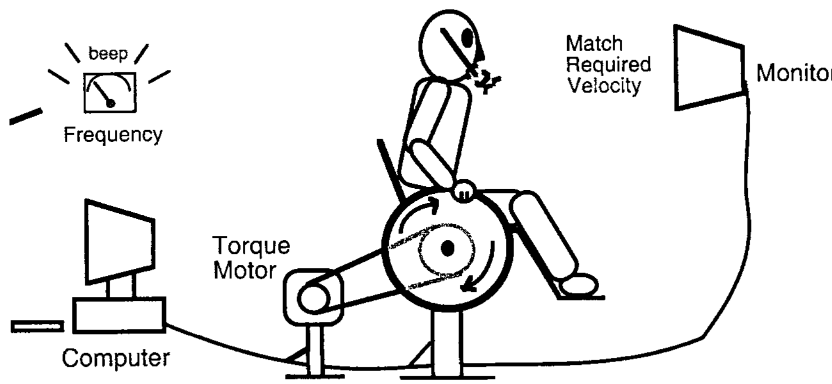

Figure 1. Experimental arrangement for the study of locomotor–respiratory coupling during manual wheelchair propulsion. From "Locomotor–Respiratory Coupling During Manual Wheelchair Propulsion," by P. G. Amazeen, E. L. Amazeen, and P. J. Beck, 1999. In L. H. V. van der Woude, M. T. E. Hopman, and C. H. van Kemenade (Eds.), *Ergonomics of Manual Wheelchair Propulsion: State of the Art II* (p. 203), Amsterdam, the Netherlands: IOS Press. Copyright 1999 by IOS Press. Reprinted with permission.

mounted in a mouthpiece registered the flow at 100 Hz. The mouthpiece was attached to a headband that the participant wore, and a nose clip was used to guarantee oral respiration. The propulsion and respiratory time series were synchronized. Analyses were conducted to identify the onset of respiratory and propulsion cycles as sharp, positive accelerations of the respiratory and propulsion time series, respectively. (Raw data are presented in Figure 2.)

Algorithms. An 18-point running average was computed to smooth both the respiratory and propulsion time series. The first derivative of these smoothed time series was calculated, and maximal accelerations were identified as the onset of inspiration and the onset of propulsion, respectively. Respiratory and propulsion frequencies were calculated cycle-by-cycle as the sampling frequency (100 Hz in Experiment 1; 50 Hz in Experiments 2 and 3) divided by the difference between one onset and the preceding cycle's onset. Each of these frequency time series was expanded to a time series of 12,000 points so that we could determine both the frequency ratio and relative phase. In addition, we represented the propulsion phase with a number between 0° and 360°, with 0° set as the onset and 360° set as the termination of each propulsion cycle.

Both frequency ratio and relative phase were calculated using the onset of inspiration as a landmark. Effectively, then, there were as many frequency ratio and relative phase calculations as there were respiratory cycles for each trial. Frequency ratio was calculated by dividing the propulsion frequency by the respiratory frequency at the onset of inspiration. Relative phase was defined as the propulsion phase minus the respiratory phase. We identified this as the phase of propulsion at the onset of inspiration. On the basis of this convention, a positive relative phase value was indicative of the propulsion cycle being initiated prior to inspiration, and a negative relative phase value was indicative of the propulsion cycle being delayed until after the onset of inspiration.

Procedure. Prior to the experiment, each participant's maximum load (ML) was determined so that manipulations of the wheelchair's rolling resistance (in newton meters) could be scaled to individual abilities. ML was operationally defined as the maximum rolling resistance for which a participant could sustain a maximum velocity of 6.5 km/hr (the maximum velocity used in the experiment) for 5 min. ML varied widely across participants (26–40 Nm across both left and right wheels). Participants were also given an opportunity, on a separate trial, to adjust to the mouthpiece by breathing through it for a period of 5 min. Once the experiment began, the mouthpiece was worn during each 5-min trial. On any given trial, each participant sustained a constant velocity of 3.6, 5.0, or 6.5 km/hr at one of three loads (10 Nm, 0.5 ML, or 1.0 ML). The two lower velocities were within the range of velocities used in previous experiments on wheelchair propulsion in both spinal cord injured and able-bodied participants (e.g., Dallmeijer, van der Woude, Hollander, & Angenot, 1999; van der Woude et al., 1999; van der Woude, Veeger, Rozendal, & Sargeant, 1989); we included the highest velocity condition to test the possibility that LRC might occur only during extreme testing conditions. Because of technical limitations on the total sample size, data were collected at 100 Hz during the last 40 s of the 2nd, 3rd, 4th, and 5th min of each trial, yielding propulsion and respiratory time series of 4,000 data points each. Trial order was randomized and participants were permitted to rest after each trial for at least 5 min. The experiment was conducted in two 1-hr sessions on 2 different days so that we could avoid the effects of fatigue. All procedures reported in the present experiments adhere to the ethical guidelines of the American Psychological Association. They were approved by the Research Committee of the Faculty of Human Movement Sciences of the Vrije Universiteit, Amsterdam.

Results

Figure 2 depicts the raw, unsmoothed time series for two representative participants. Note that each point of inhalation, which marks the onset of the respiratory cycle, is accompanied by a push to the right wheel rim. There are consistently two propulsion cycles per respiratory cycle (i.e., a 2:1 frequency ratio) in Figure 2A and four propulsion cycles per respiratory cycle (4:1) in Figure 2B. In both instances, the onset of the respiratory cycle is temporally synchronized with the onset of the propulsion cycle. This inphase relation is depicted in Figure 3 for the 2 more experienced and the 5 less experienced (novice) participants. Relative phase is displaced slightly in the positive direction for novices, revealing a preference for initiating the propulsion cycle slightly prior to inhaling, and in the negative direction for more experienced wheelchair users, indicating that they tended to delay the propulsion cycle until the onset of inspiration. The reliability of this observation was tested when experience was manipulated explicitly in Experiment 2.

The ratio of propulsion to respiratory frequency was calculated for every respiratory cycle individually. Because the number of respiratory cycles differed widely across individuals (2–20 for 40 s), the frequency distributions of Figures 4A–4H depict the percentage of the total number of cycles that were spent perform-

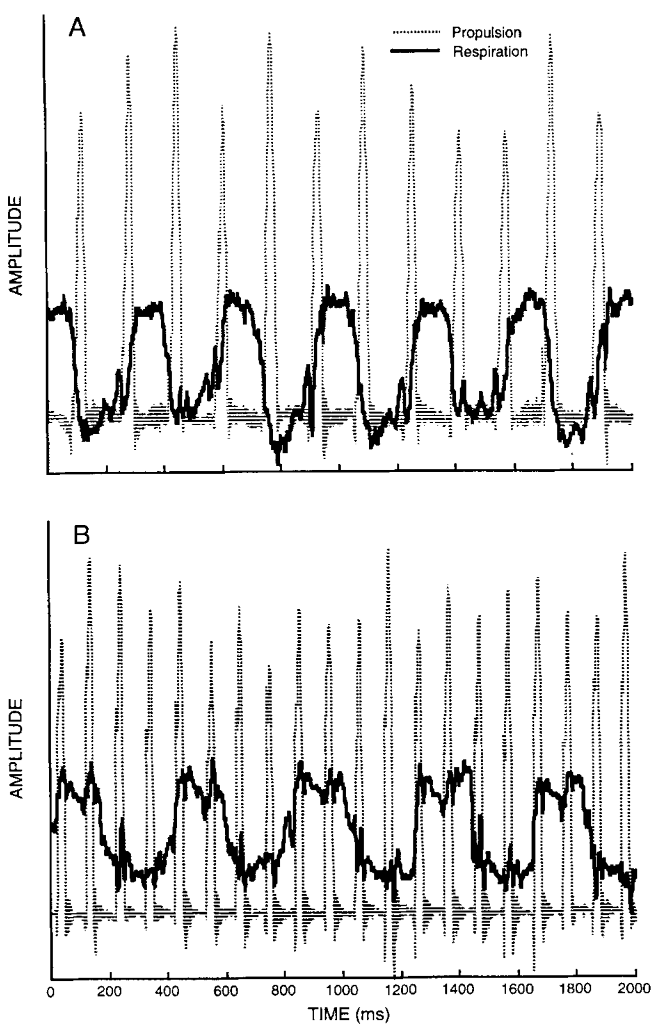

Figure 2. Raw, unsmoothed time series of propulsion and respiration for 2 representative participants maintaining 2:1 (A) and 4:1 (B) in Experiment 1. From "Locomotor-Respiratory Coupling During Manual Wheelchair Propulsion," by P. G. Amazeen, E. L. Amazeen, and P. J. Beck, 1999. In L. H. V. van der Woude, M. T. E. Hopman, and C. H. van Kemenade (Eds.), *Ergonomics of Manual Wheelchair Propulsion: State of the Art II* (p. 204), Amsterdam, the Netherlands: IOS Press. Copyright 1999 by IOS Press. Reprinted with permission.

ing the different frequency ratios. The percentage of cycles in the area under each peak was estimated by adding the cycles accounted for by the local maximum ± 0.2 (see Table 1; only values greater than 10% are reported). The two more experienced individuals (Figures 4A and 4B) consistently produced a 2:1 frequency ratio; the peaks at 2:1 account for over 60% of the cycles performed. In addition, the individual in Figure 4B performed a 3:2 ratio, as indicated by a peak that is centered at 1.5, for 27% of all cycles. The performance of less experienced individuals was more variable. The novice in Figure 4C demonstrated a clear preference for 4:1 and 6:1 frequency ratios, whereas all other novices (Figures 4D–4G) consistently produced 2:1 in addition to at least one other small-integer frequency ratio (3:1, 4:1, 3:2, or 5:2). It is notable that in contrast to the more experienced wheelchair users, none of the peaks accounts for more than 40% of the cycles performed, although combining all peaks accounts for an average of at least 50% of performance. Given that experience appears to be a relevant variable, we combined individual performance post hoc according to level of experience in Figure 4H. Note that although LRC appears to occur for both groups, performance is more clearly defined and less variable for more experienced wheelchair users. The reliability of this observation was tested when experience was manipulated explicitly in Experiment 2.

An analysis of variance (ANOVA) was performed to determine the effect of velocity and rolling resistance on respiratory frequency, propulsion frequency, and the ratio of the two. Although both respiratory frequency (M = 0.264, 0.288, and 0.328 Hz for 3.6, 5.0, and 6.5 km/hr, respectively) and propulsion frequency (M = 0.684, 0.760, and 0.858 Hz for 3.6, 5.0, and 6.5 km/hr, respectively) increased significantly with increased velocity, $F(2, 12) = 8.73, p < .005$ and $F(2, 12) = 11.70, p < .005$, respectively, the cycle-by-cycle frequency ratio was unaffected by the velocity manipulation, $F(2, 12) < 1$. This replicates MacDonald et al.'s (1992) finding of a lack of influence of velocity on LRC. An increase in rolling resistance was accompanied by an increase in only the frequency of propulsion (M = 0.708, 0.750, and 0.836 Hz for 10 Nm, 0.5 ML, and 1.0 ML, respectively), $F(2, 12) = 5.04$, $p < .005$, and did not affect the cycle-by-cycle frequency ratio, $F(2, 12) < 1$. Therefore, although manipulations of both velocity and rolling resistance bring about changes in other relevant measures in wheelchair propulsion (e.g., gross mechanical efficiency; van der Woude et al., 1988), they do not alter the LRC pattern.

Discussion

The results of Experiment 1 demonstrate, in contrast to the findings of MacDonald et al. (1992), that LRC does occur during manual wheelchair propulsion. The phasing of the coupling was such that novices tended to initiate the propulsion cycle prior to inspiration, whereas more experienced wheelchair users tended to inspire just prior to initiating the push on the wheel rim. Frequency coupling was markedly different in that more experienced wheelchair users tended to maintain a 2:1 ratio during most of each experimental run, whereas novices tended to alternate between 2:1 and at least one other frequency ratio (e.g., 3:1, 4:1, 6:1, 3:2, or 5:2). Although altering frequency ratios has been demonstrated in past experiments on running and bicycling (Bramble & Carrier, 1983; Garlando et al., 1985; Paterson et al., 1986), studies on elite rowers and on the acquisition of rowing have demonstrated that maintenance of a single frequency ratio may be preferable for upper-limb activities (Mahler, Hunter, et al., 1991; Mahler, Shuhart, et al., 1991). The lack of experience with the task possibly prevented novices from being able to vary both their rate of propulsion and respiration simultaneously to hold the ratio between them constant. Alternatively, a more effective movement manipulation may allow both experienced and novice wheelchair users to demonstrate a systematic shift in both frequency ratios and the phasing of the coupling.

The results of Experiment 1 indicate that the visceral piston, which relies on the vertical impulse that is produced during lower-limb activity, is not the sole mechanism for LRC. The possibility exists that some other mechanical perturbation—perhaps the

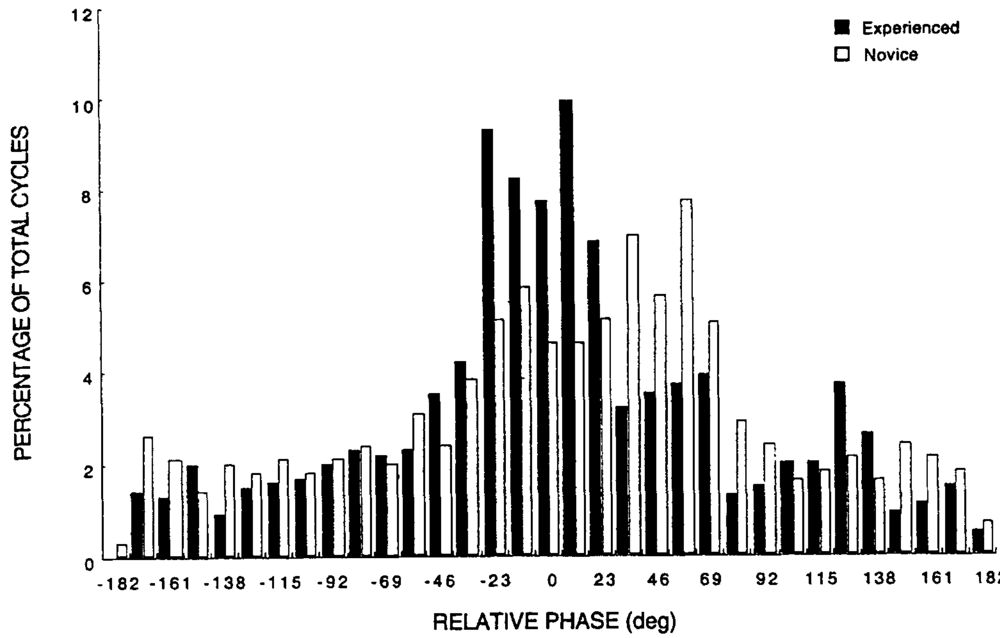

Figure 3. The percentage of all cycles at which a given phase relation between propulsion and respiration was maintained by more experienced wheelchair users and novices in Experiment 1. deg = degrees.

rhythmic movements of the upper limbs or the rhythmic tightening of the abdominal muscles during the task—may drive the coupling. There is evidence from the motor coordination literature that the same coordination patterns are observed when limbs are coupled haptically (neurally) or visually (e.g., Amazeen et al., 1995; Schmidt et al., 1990). This indicates that coupling may be informationally based; that is, there must be some information exchange between the component systems that need not be mechanical in nature.

A number of studies have identified important kinematic differences in propulsion technique between wheelchair-dependent and able-bodied individuals (e.g., Brown, Knowlton, Hamill, Schneider, & Hetzler, 1990; Veeger et al., 1992). For example, able-bodied individuals tend to initiate the push later, have a greater shoulder range of motion, and lean forward further than do wheelchair-dependent individuals (Veeger et al., 1992). However, without a clear experimental separation between level of experience and motor dysfunction it is difficult to identify those aspects of the kinematics that might result in the coupling differences that were observed among able-bodied individuals in Experiment 1. The alternative to a mechanically based coupling is that LRC is produced by parallel control of movement and respiration, perhaps inherent in the neurophysiological control of muscles that drive both processes. Only partial support has been given to this latter argument in animal experiments (Eldridge, Millhorn, Kiley, & Waldrop, 1985; Iscoe & Polosa, 1976; Viala, 1986; Viala & Freton, 1983; Viala, Vidal, & Freton, 1979). The argument for some form of parallel control is made stronger, however, in the absence of alterations to LRC as a result of direct changes in the movement pattern, as should have occurred during velocity and rolling resistance manipulations (e.g., van der Woude et al., 1988). Instead, the only systematic changes in LRC appeared to have come from experience, a hypothesis that we tested explicitly in Experiment 2. The addition of a more effective movement manipulation may also shed light on the directionality of the coupling.

Experiment 2: Manipulation of Movement Frequency

Although LRC was observed in the first experiment, manipulations of the traditional wheelchair propulsion variables of velocity and rolling resistance failed to bring about any changes to the resulting frequency ratios. Manipulations of velocity cause a shift from 4:1 to 2:1 in experienced runners (Bramble & Carrier, 1983). However, rowers tend to not shift their ratios at different velocities (Mahler, Shuhart, et al., 1991). Although it is possible that 1:2 or 2:1 is the preferred frequency ratio for LRC involving upper-limb activities, it is also possible that other movement variables, such as movement frequency, may influence LRC. In the motor coordination literature, movement frequency has been shown to cause qualitative shifts in the phasing (e.g., Kelso, 1984) and the frequency ratio of two-limb movements (e.g., Haken, Peper, Beek, & Daffertshofer, 1996; Peper et al., 1995a). In multifrequency coordination in particular, an increase in movement frequency is accompanied by the shift to smaller-integer rather than to larger-integer frequency ratios (Haken et al., 1996; Peper et al., 1995a; Treffner & Turvey, 1993). If a similar trend is found in LRC, then a single modeling strategy may be used for coordination both within the motor subsystem and between it and other physiological subsystems of the body.

In the physiological literature, increases in movement frequency have been shown to cause increases in the amount of oxygen consumed ($\dot{V}O_2$) during upper-limb tasks such as arm cranking (e.g., Weissland et al., 1997) and wheelchair propulsion (e.g., van der Woude et al., 1989). Therefore, we manipulated movement

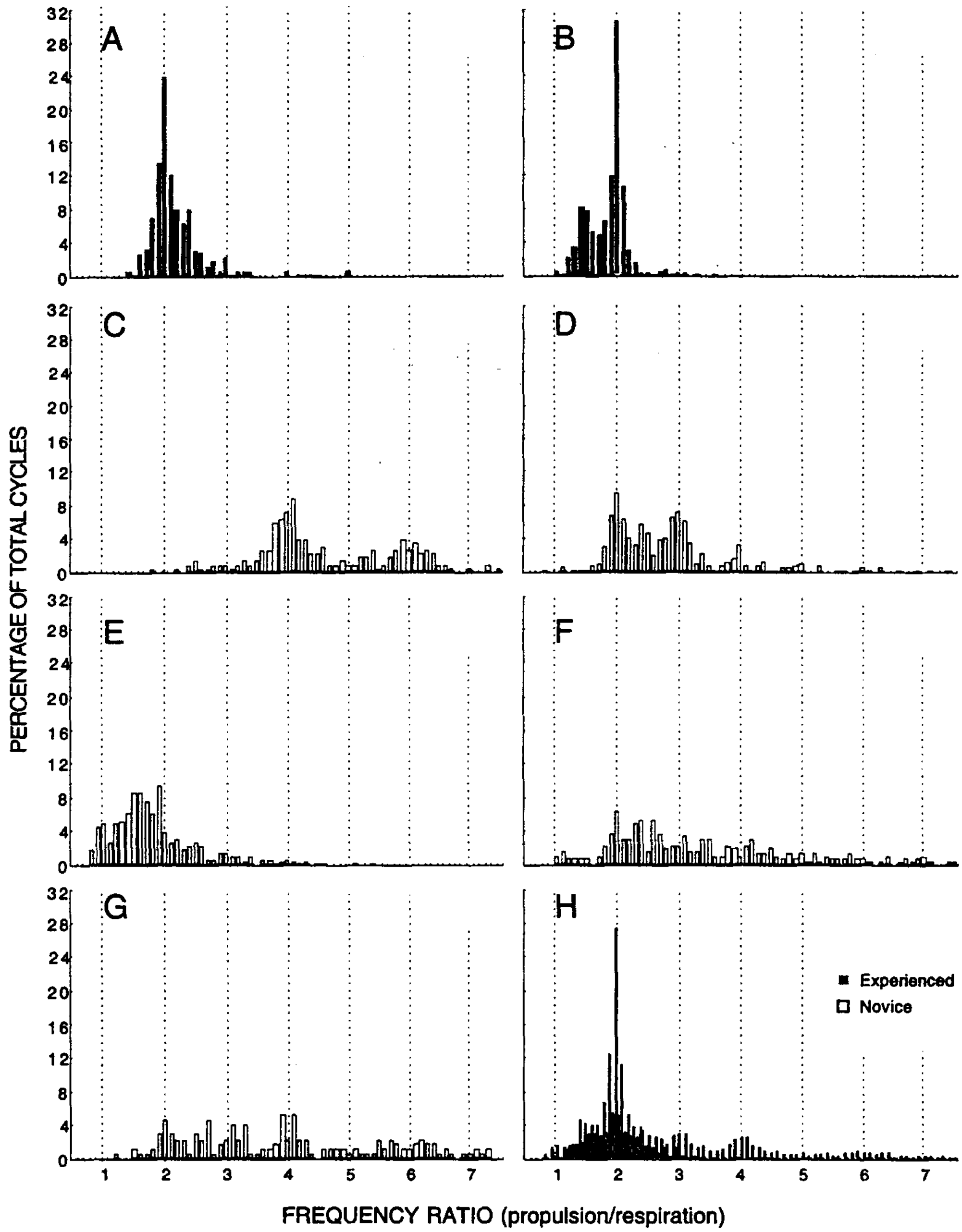

Figure 4. Frequency distribution of frequency ratios produced by all participants in Experiment 1 individually (A–G) and by the group (H), which was divided post hoc into more experienced wheelchair users and novices.

frequency in Experiment 2—following the scaling procedure of van der Woude et al. (1989)—to determine whether variations in movement frequency would bring about shifts in the phasing or frequency coupling of propulsion and respiration. In addition, level of experience was manipulated explicitly to clarify the findings of Experiment 1 that both phasing and frequency coupling may be dependent on experience with the propulsion task.

Method

Participants. Participants were 6 able-bodied experienced wheelchair users (5 men; 1 woman; 19–44 years old; all right-handed) and 8 able-bodied novices with no prior wheelchair experience (3 men; 5 women; 19–34 years old; all right-handed). Participants were asked to refrain from smoking and from ingesting caffeine and/or alcohol for at least 2 hr prior to testing. They were asked to eat a light meal 2 hr before the experiment. They were paid 12.50 Nlg (approximately $6.25) per hour for their participation. All participants signed an informed consent form, which indicated that they could terminate participation at any time without penalty. Because of a shortage of able-bodied participants with previous wheelchair experience, 2 experienced wheelchair users from Experiment 1 participated in Experiment 2. The 4 other experienced wheelchair users had previously participated in a 7-week wheelchair training study on physical work capacity (van der Woude et al., 1999). With the exception of the 2

Table 1
Percentage of Time Spent Performing a Given Frequency Ratio by Experienced Wheelchair Users and Novices in Experiment 1

	Ratio						
Participant	2:1	3:1	4:1	6:1	3:2	5:2	Total
Experienced							
1	64	—	—	—	—	—	64
2	62	—	—	—	27	—	89
Novice							
1	—	—	30	14	—	—	44
2	29	27	—	—	—	—	56
3	29	—	—	—	36	—	65
4	18	11	—	—	—	20	49
5	14	14	16	—	—	12	56

Note. Dashes indicate a percentage of less than 10.

participants from Experiment 1, all other participants were naive to the purpose of the experiment. To retain the distinction between experienced and novice participants, we did not permit any of the participants to practice with the equipment prior to the experiment.

Apparatus. The experiment was conducted using the wheelchair ergometer and pneumotachometer described in Experiment 1. An auditory metronome was used to pace the propelling frequency.

Procedure. On a day prior to testing, an isometric strength test was conducted to determine each participant's maximal power output (PO_{max}) in accordance with the protocol described in van der Woude et al. (1999). No mouthpiece was worn. With the results of the isometric strength test, individual PO_{max} was estimated using an equation calculated by Janssen et al. (1993) to be strongly and positively correlated ($r = 0.81$) with direct measurements of PO_{max}. PO_{max} estimates are reported in Table 2. The values for novice and experienced wheelchair users are consistent with the pretraining and posttraining estimates for able-bodied participants in van der Woude et al. (1999), with PO_{max} significantly lower for novices than for experienced wheelchair users, $t(12) = 2.29, p < .05$. While PO_{max} was being calculated, participants were permitted to propel the wheelchair at a comfortable speed and with a comfortable propulsion frequency for 6 min, with the rolling resistance of the wheelchair set at the minimum (10 Nm). Thereafter, the rolling resistance of the wheelchair was held constant across trials so that the individual's power output during the highest velocity condition was 50% PO_{max}. Individual PO_{max} estimates are reported in Table 2. If the participant experienced any difficulty in completing the high-velocity trial, then the rolling resistance was reduced to require a power output of 40% PO_{max} for that condition. We expected to make some adjustments for a small percentage of participants because we used an estimate of PO_{max}; the adjustment was performed for 2 experienced wheelchair users (1 and 5) and 1 novice (2).

Each of the velocity conditions (3, 4, and 5 km/hr) was then presented in a random order to determine the participant's preferred frequency of propulsion for each of the velocities. Preferred frequencies of propulsion are reported in Table 2. Propulsion frequencies for the 3 participants for whom the rolling resistance was reduced were indistinguishable from the remainder of the participants, indicating that the pattern of results was not compromised by the adjustment. Although the participant profile and experimental conditions vary somewhat, these values are within the range reported for the same velocity conditions in van der Woude et al. (1989). As in past studies (e.g., van der Woude et al., 1989), the preferred frequency of propulsion increased with increases in velocity, $F(2, 24) = 9.67, p < .001$. The difference found between experienced wheelchair users and novices was not significant, $F(1, 12) = 3.38, p > .05$.

Before the experiment began on the second day, participants were given an opportunity to adjust to the mouthpiece by breathing through it for a period of 6 min. Once the experiment began, the mouthpiece was worn during each 6-min trial. On any given trial, each participant sustained a constant velocity of 3, 4, or 5 km/hr at either their preferred frequency of propulsion or 20% below or above their preferred frequency of propulsion for that particular velocity; both the velocity selection and frequency scaling followed the experimental protocol of van der Woude et al. (1989). The last 4 min of each trial were recorded at 50 Hz. Sampling frequency was decreased from 100 Hz because details in neither the respiratory nor the propulsion time series of Experiment 1 were sufficiently coarsely grained to require greater precision. Trial order was randomized and participants were permitted to rest after each trial for at least 5 min. The experiment was conducted in two 1-hr sessions on 2 different days so that we could avoid the effects of fatigue.

Results

One of the observations in Experiment 1 was that although the onsets of the respiratory and propulsion cycles were synchronized—that is, although they were centered about inphase—more experienced wheelchair users tended to initiate their respiratory cycle slightly prior to their propulsion cycle, whereas novices tended to initiate their propulsion cycle slightly prior to their respiratory cycle. The level of experience of participants was manipulated in the present experiment so that its influence on the phasing of propulsion and respiration could be tested explicitly. Figure 5 depicts a histogram of relative phase calculations across trials for both experienced and novice participants. Notice that the distribution of phase relations is displaced in the positive direction ($M = 13°$), implying that both experienced and novice participants were beginning their push on the wheel rim before they started to inhale.

Means and ANOVAs are presented in Table 3. An ANOVA revealed no significant differences between the two groups, so that

Table 2
Individual Differences in the Estimates of PO_{max} and Preferred Propulsion Frequencies in Experiment 2

		Preferred frequency (Hz)		
Participant	PO_{max} (W/kg)	3 km/hr	4 km/hr	5 km/hr
Experienced				
1	1.46	0.98	0.96	0.97
2	1.27	0.72	0.79	0.85
3	0.91	0.85	0.72	0.80
4	1.49	0.98	0.94	0.96
5	1.02	0.76	0.79	0.88
6	1.09	0.62	0.73	0.83
Novice				
1	0.65	1.26	1.43	1.36
2	1.00	0.86	0.93	0.84
3	0.88	0.93	1.13	1.28
4	0.98	1.37	1.38	1.43
5	0.71	0.83	0.96	1.04
6	0.68	0.65	0.78	0.77
7	1.04	0.93	1.08	1.06
8	1.36	0.67	0.80	1.02

Note. PO_{max} = participant's maximal power output.

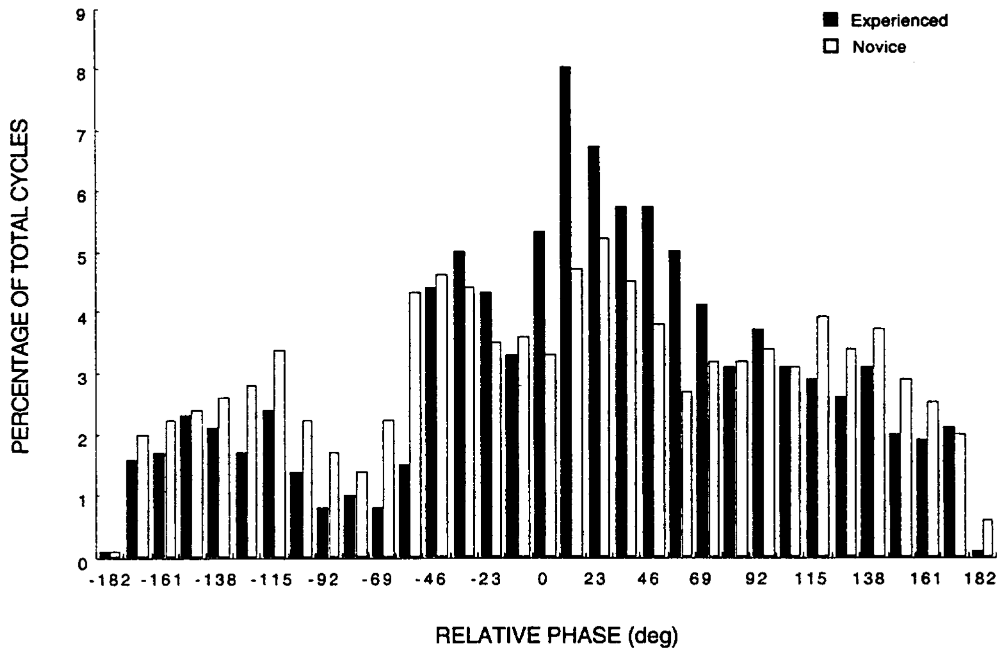

Figure 5. The percentage of all cycles at which a given phase relation between propulsion and respiration was maintained by experienced wheelchair users and novices in Experiment 2. deg = degrees.

experience appears to not have played a role in the phasing of propulsion and respiration. Relative phase was only affected by the velocity manipulation, such that higher velocities tended to drive relative phase closer to zero. That is, respiration and propulsion were more synchronized at higher velocities. Although the propulsion frequency did not affect the relative phase directly, participants elected a higher propulsion frequency for higher velocities. This effect was demonstrated previously for both wheelchair sportsmen and nonwheelchair users (van der Woude et al., 1988, 1989). It is possible that propelling the wheelchair more quickly caused the propulsion cycle to start a bit later and, therefore, closer to the onset of the respiratory cycle.

The ratio of propulsion to respiratory frequency was calculated cycle by cycle and is presented as a percentage of occurrence for low, medium, and high propulsion frequency trials for 3 of the more experienced individuals (Figure 6) and 3 novices (Figure 7). Note that each participant tended to prefer a 2:1 and, in some cases, a 3:1 ratio at low and medium frequencies of propulsion and shifted to a 3:1 and, in Figure 6C, a 4:1 ratio at the highest propulsion frequency. The same trend appears

Table 3
Means and Analysis of Variance Results for the Measures of Relative Phase, Propulsion Frequency, Respiratory Frequency, and Frequency Ratio in Experiment 2

		Means (or *F* values)			
Manipulation	*df*	Relative phase (deg)	Propulsion frequency (Hz)	Respiratory frequency (Hz)	Frequency ratio
Experience	1, 12	(<1)	(3.50)	(2.92)	(<1)
Experienced		19	0.848	0.349	2.64
Novice		8	1.038	0.441	2.54
Velocity (km/hr)	2, 24	(4.85)*	(6.40)**	(14.47)***	(1.53)
3		20	0.899	0.380	2.57
4		13	0.948	0.386	2.68
5		8	0.982	0.421	2.53
Propulsion frequency (% preferred)	2, 24	(<1)	(142.33)***	(7.05)**	(22.22)***
80		13	0.774	0.366	2.31
100		15	0.939	0.401	2.57
120		12	1.114	0.419	2.89

Note. deg = degrees.
* $p < .05$. ** $p < .01$. *** $p < .0001$.

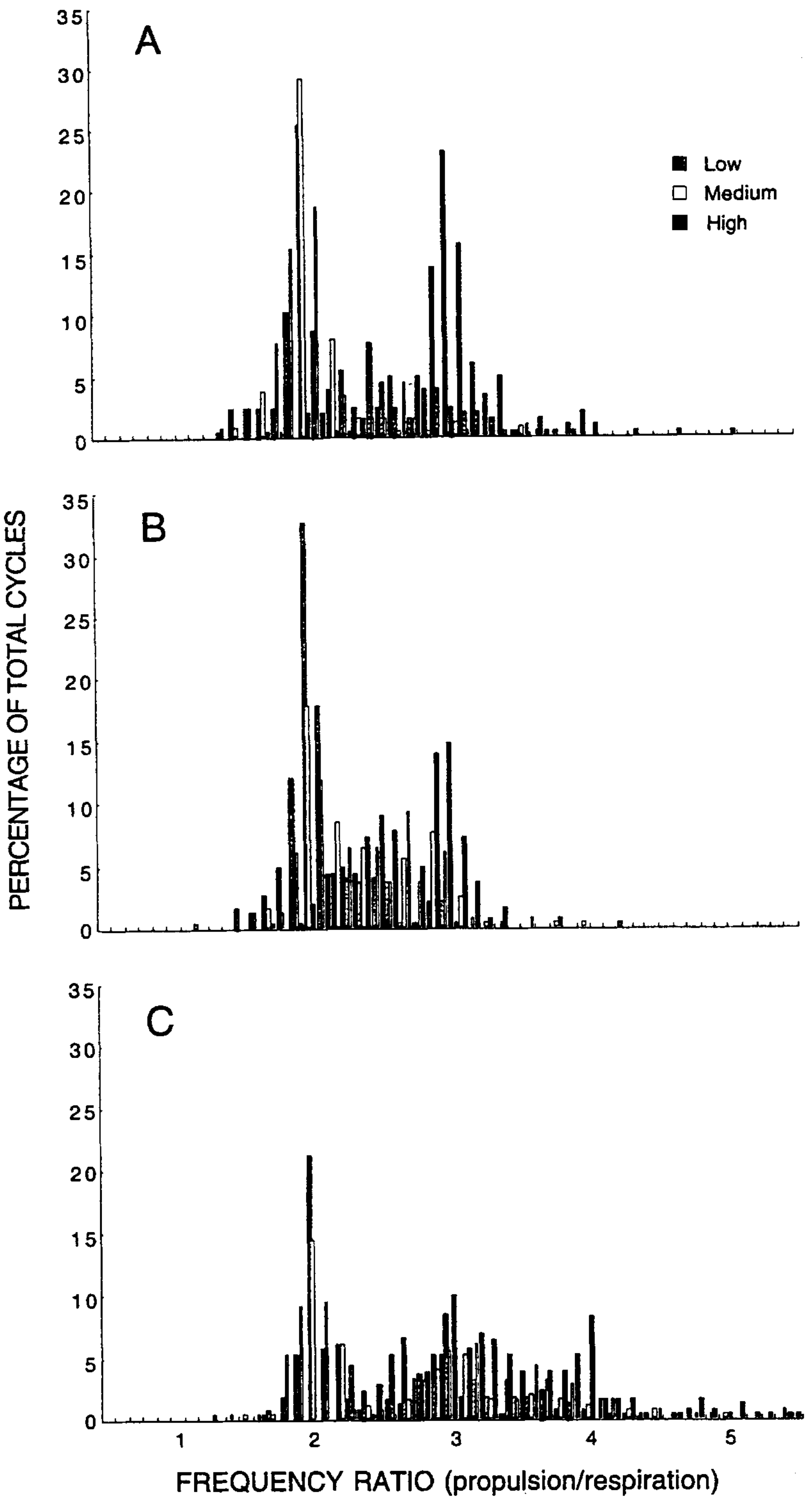

Figure 6. Frequency distribution of frequency ratios produced at low (80%), medium (100%), and high (120%) frequencies of propulsion by 3 experienced wheelchair users in Experiment 2.

across the two groups in Figure 8 and in Table 4. As in Experiment 1, the number reported in Table 4 is the percentage of cycles (>10%) in the area under each peak. Experienced wheelchair users produced a 2:1 ratio at all three frequencies of propulsion, but the percentage of cycles accounted for by the 2:1 peak decreased at the highest frequency. This decrease was accompanied by the growth of a peak at 3:1 during medium and high propulsion frequency trials. During the fastest propulsion

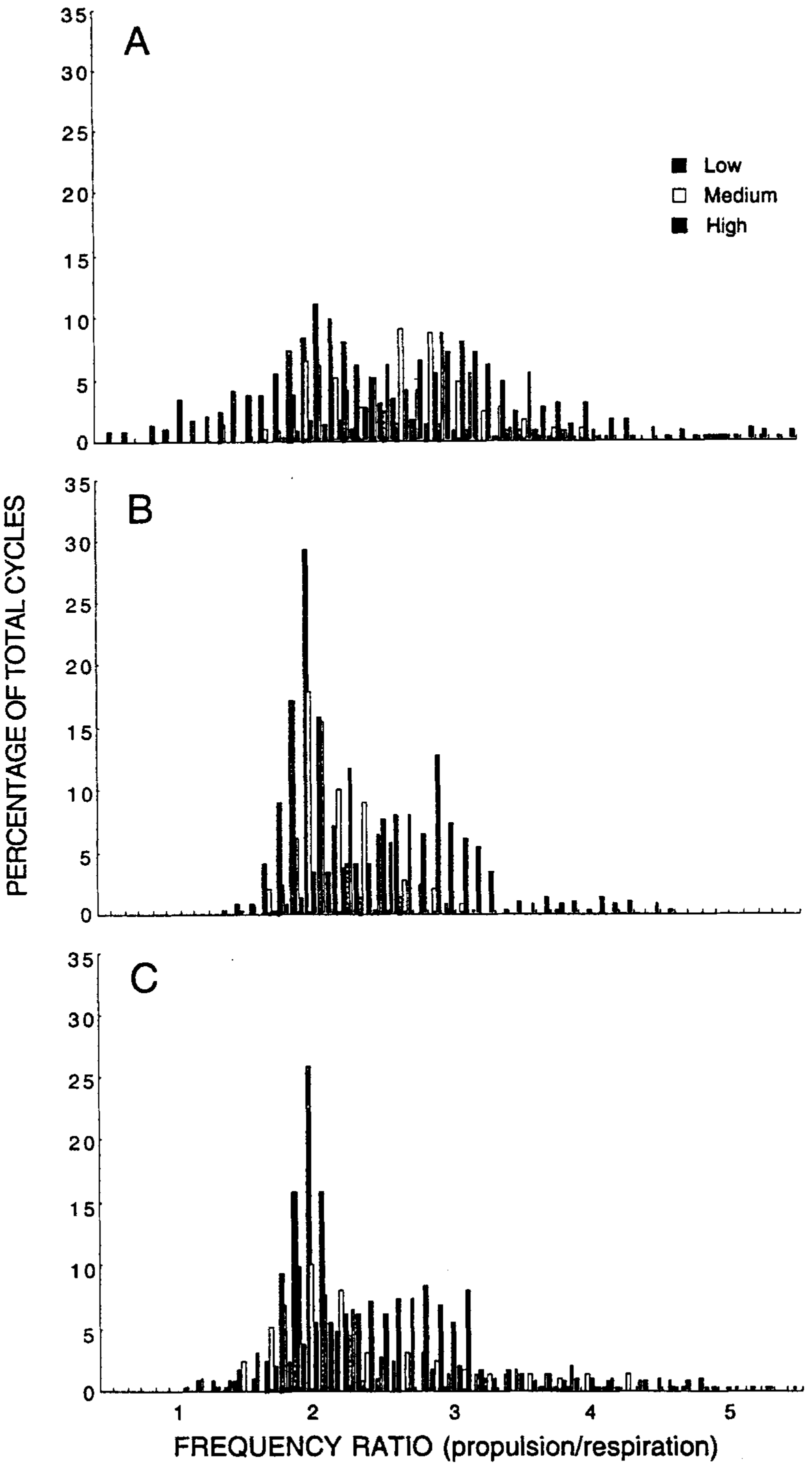

Figure 7. Frequency distribution of frequency ratios produced at low (80%), medium (100%), and high (120%) frequencies of propulsion by 3 novices in Experiment 2.

trial, a small peak is apparent at 4:1 in Figure 8A; however, it accounted for less than 10% of the cycles produced. The same pattern was demonstrated by novices in Figure 8B: The peak at 2:1 decreased and was accompanied by the growth of a peak at 3:1 at the highest propulsion frequency. Through these frequency distributions, it is evident that although performance appears to be more clearly defined (by means of sharper peaks), for experienced wheelchair users, the constraints of the present experiment were sufficient to allow both experienced and novice participants to demonstrate LRC. Further, although complex

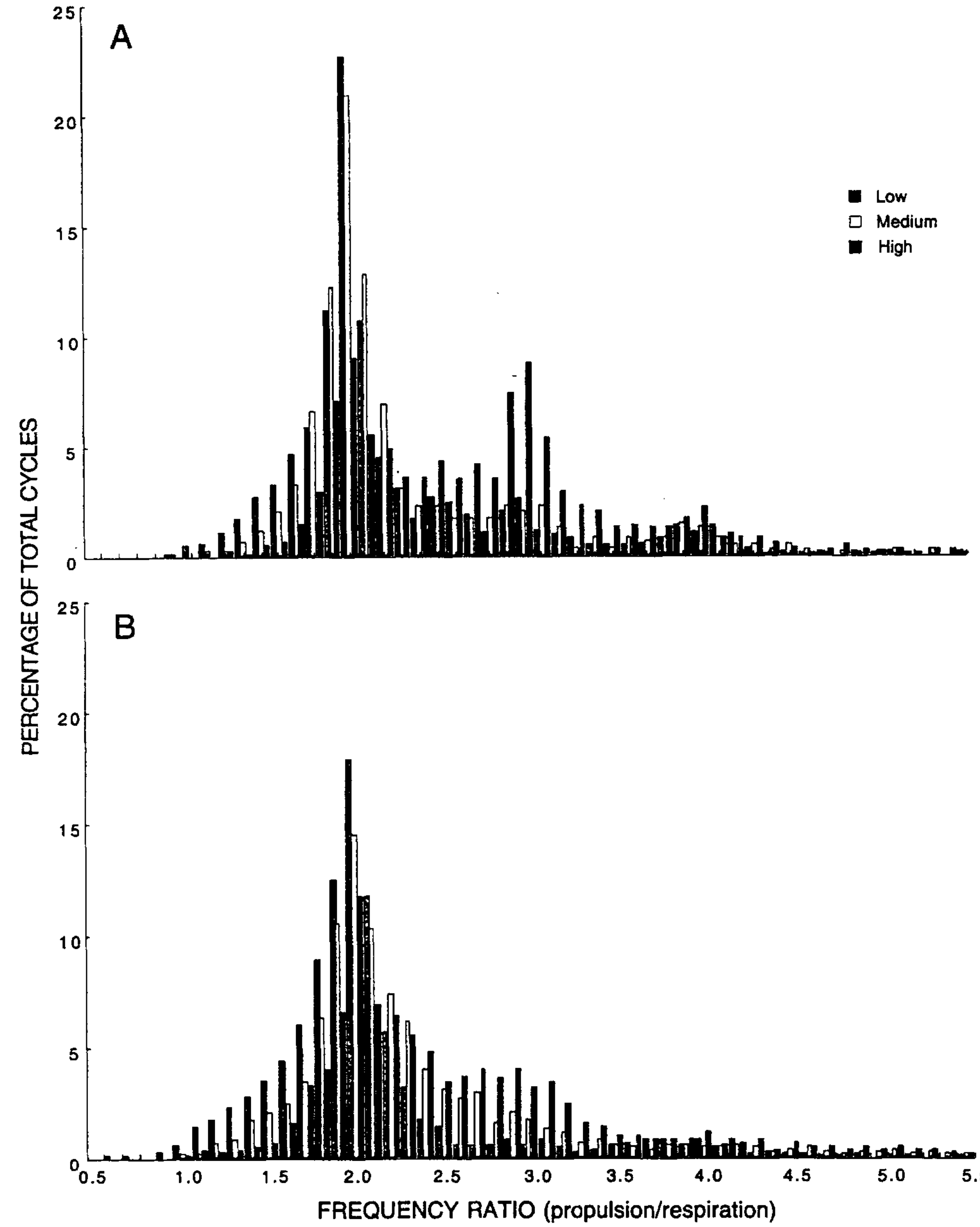

Figure 8. Frequency distribution of frequency ratios produced at low (80%), medium (100%), and high (120%) frequencies of propulsion by experienced wheelchair users (A) and novices (B) in Experiment 2.

frequency ratios like 3:2 and 5:2 were observed in Experiment 1, holding propulsion frequency constant during a trial appears to have limited performance to the low, simple frequency ratios of 2:1, 3:1, and 4:1.

ANOVAs (Table 3) were conducted to determine the influence of propulsion frequency and velocity on the respiratory frequency, propulsion frequency, and the ratio of the two. Increases in the frequency of propulsion were accompanied by increases in respiratory frequency. A manipulation check performed on the propulsion frequency measure revealed the expected increase. Although both respiratory frequency and propulsion frequency increased, the cycle-by-cycle ratio of the two increased as well. An ANOVA revealed the main effect of propulsion frequency to be significant both for the mean frequency ratio and for the variability (standard deviation) of frequency ratios produced within the trial (0.40, 0.48, and 0.56 for 80%, 100%, and 120%, respectively), $F(2, 24) = 12.04$, $p < .0002$. That is, frequency ratios increased in value and became more variable with increases in the propulsion frequency. In Figure 8, this is observed in the transition from a unimodal distribution at the lowest propulsion frequency to a bimodal or trimodal distribution at the highest propulsion frequency.

Table 4
Percentage of Time Spent Performing a Given Frequency Ratio by Experienced Wheelchair Users and Novices for Three Frequencies of Propulsion in Experiment 2

Frequencies of propulsion (% of preferred)	Ratio 2:1	3:1	Total
Experienced			
80	55	—	55
100	60	10	70
120	29	28	57
Novice			
80	57	—	57
100	49	—	49
120	36	18	54

Note. Dashes indicate a percentage of less than 10.

In replication of the results of Experiment 1, increases in the wheelchair's velocity were accompanied by a significant increase in both respiratory frequency and propulsion frequency, but they did not affect the cycle-by-cycle frequency ratio.

Discussion

The results of Experiment 2 replicate the results of both MacDonald et al. (1992) and Experiment 1 in demonstrating the lack of an influence of velocity on LRC. Movement frequency, a variable previously untested in the LRC literature, clearly plays an important role in producing shifts from one frequency ratio to another. Both experienced wheelchair users and novices demonstrated a shift from 2:1 to 3:1 with increases in movement frequency, with propulsion being initiated slightly prior to inspiration. Although both simple (2:1, 3:1, 4:1, and 6:1) and complex ratios (3:2 and 5:2) were witnessed in Experiment 1, the increased constraint of maintaining a single propulsion frequency during the course of the present experiment may have played a role in bringing out the distinct preference of participants for small-integer simple ratios.

Movement frequency is an important variable in the field of motor coordination (e.g., Haken et al., 1996; Kelso, 1984) and demonstrates its generality by playing an important role in the coordination between two physiological subsystems of the body. In bimanual coordination, an increase in movement frequency is accompanied by the shift to smaller-integer rather than to larger-integer frequency ratios (Haken et al., 1996; Peper et al., 1995a; Treffner & Turvey, 1993). These transition routes may be expressed by a mathematical structure called the Farey tree (e.g., González & Piro, 1985; Hardy & Wright, 1938), an ordering of integer ratios that corresponds empirically to relative stability when it is applied to real-world phenomena (e.g., Stewart, 1989; Treffner & Turvey, 1993). The first five levels of the Farey tree are depicted in Figure 9. The lowest order level (Level 0) of the Farey tree contains the parent ratios 0:1 and 1:1. Farey summation of the parents—i.e., adding the numerators and denominators—produces one ratio, 1:2, at the next level (Level 1). Subsequently higher order levels are produced by performing Farey summations across all pairs of parents in lower order levels, so that a tree of ratios is produced, with small-integer ratios at the lower order levels and large-integer ratios at higher order levels (e.g., Hilborn, 1994). This tree structure is used to make predictions regarding both performance difficulty and transition pathways.

Although the transition route from 2:1 to 3:1, and then perhaps to 4:1 (as indicated by the emergence of a peak in Figure 8), is represented in the Farey tree, transitions would be expected to occur in the opposite direction in the coordination between two limbs of the body. This points to an interesting difference in the coordination within a single physiological subsystem of the body and between subsystems, as in LRC. Because of natural timing differences, one subsystem—in this case, the motor subsystem—may be able to change more rapidly than the other, inducing shifts in the timing relation that may be opposite to what may occur between homogeneous members of a single physiological subsystem. In Experiment 2, the frequency of respiration increased with increases in propulsion frequency, but it did so disproportionately, resulting in a significant increase in the frequency ratio. The significance of this observation lies not in the ratio increase, but in the fact that simple ratios were maintained; this indicates that once respiratory frequency increased slightly, participants must have shifted to a significantly higher respiratory frequency to maintain either a 2:1 or a 3:1 ratio. This was observed in both experienced wheelchair users and novices.

Regardless of the level of experience, all individuals demonstrated an effect of velocity on only relative phase, such that propulsion and respiration were more inphase at higher velocities. There was no further support for the observed effect of expertise on phasing in Experiment 1. Instead, all participants tended to initiate the propulsion cycle prior to inspiration. This indicates, together with the finding that manipulations of movement frequency influence LRC that the causality may be unidirectional, that is, the respiratory pattern may be dependent on the movements of the body. Although Experiment 1 and findings from the sport of rowing (Mahler, Hunter, et al., 1991; Mahler, Shuhart, et al., 1991) demonstrate that the visceral piston cannot be the only mechanism for LRC, it is still possible that the movements of upper or lower limbs mechanically perturb the diaphragm so as to induce a coupling between propulsion (or locomotion) and respiration.

Experiment 3: Manipulation of Inspiration

In Experiment 2, manipulation of the characteristics of the motor system—specifically, the frequency of propulsion—influenced the pattern of respiration sufficiently as to induce a change

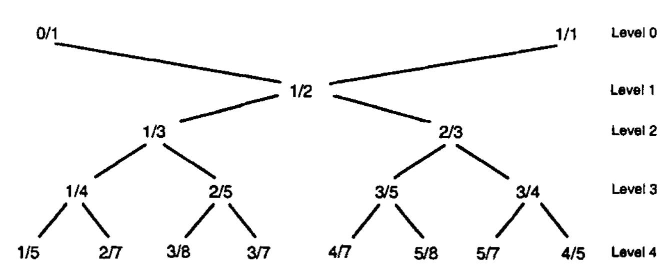

Figure 9. The Farey tree is a mathematical structure that produces all possible integer ratios through the Farey summation of two parent ratios at Level 0. Ratios at higher order levels are produced by adding the numerators and denominators of ratios at lower order levels.

in the frequency coupling of manual wheelchair propulsion and respiration. Although LRC was not produced by the vertical impulse of the lower limbs on the diaphragm, the causal influence may be unidirectional. This coincides with opinions in the literature that the movement pattern drives the respiratory pattern (e.g., Bramble & Carrier, 1983; Paterson et al., 1986). To the best of our knowledge, however, characteristics of respiration have never been directly manipulated. In the previous two experiments, challenges to the motor system came in the form of increasing power output, which includes both velocity and rolling resistance, and movement frequency. In the present experiment, a threshold inspiratory muscle trainer (IMT) was used to challenge the respiratory system by increasing the resistance to inspiration. The IMT is usually fitted to a mouthpiece, and it sets a minimal limit on the amount of inspiratory pressure that is needed before air is let through. Threshold loading is often used to test or increase the endurance of respiratory muscles, as in the training of athletes in aerobically demanding sports and in the rehabilitation of patients with chronic obstructive pulmonary disease (e.g., Gosselink, Wagenaar, & Decramer, 1996). Given the increased challenge of respiration, the only motor requirement in Experiment 3 was to keep the wheels of the wheelchair in motion. An influence on the motor output by a manipulation of respiration would indicate a possible bidirectionality in the coupling between these two physiological subsystems of the body.

Method

Participants. All experienced wheelchair users and all but 1 novice from Experiment 2 participated in Experiment 3. Preexperiment instructions and payment were the same as in Experiment 2.

Apparatus. A threshold inspiratory muscle trainer (IMT; HealthScan Products, Cedar Grove, NJ) was used to manipulate the amount of pressure that was required to inhale air from the surrounding environment. Healthy individuals have been shown to have a maximal inspiratory mouth pressure (Ptmax) of 97 ± 17 cm · H_2O (Gosselink et al., 1996). Previous studies on inspiratory loading in healthy individuals have revealed that thresholds as low as 2.5 cm · H_2O are perceived as significantly more difficult than unrestricted inspiration (Yan & Bates, 1999). Pilot testing for the present experiment revealed that 19 cm · H_2O approached the maximal inspiratory mouth pressure that could be tolerated during 5 min of wheelchair propulsion. Therefore, on any given trial, the critical threshold at which the air valve was opened was set to 0, 10, or 19 cm · H_2O, that is, 0, 10% Ptmax, or 20% Ptmax. These values were within the range of threshold loads used by Yan and Bates (1999). A butterfly valve (Astra Technologies, Rijswijk, The Netherlands) that placed restrictions on the inflow but not the outflow ensured that the participant could exhale freely. Therefore, only the difficulty of inspiration was manipulated. The threshold trainer was affixed to the distal end of the pneumotachometer so that respiratory frequency could be measured.

Procedure. Prior to testing, the physical dimensions and rolling resistance of the wheelchair ergometer were set to the same values that were used for each participant in Experiment 2. The monitor was covered so that participants had no explicit feedback regarding their velocity during the experiment. Although velocity was not manipulated explicitly, participants tended to elect a velocity that required their average power output to be 35% PO_{max}. There were no differences between novice and experienced wheelchair users regarding either the freely elected velocity, $F(1, 11) < 1$, or the percentage of PO_{max} elected, $F(1, 11) = 1.13$, $p > .05$. Before performing any propulsion trials, the participants were first given an opportunity to adjust to the threshold apparatus by breathing through the mouthpiece for three 5-min trials, one per threshold level. They were instructed to take off the nose clip at any time to terminate the trial if they experienced any discomfort (in practice, this did not happen). Participants were required to complete 5 min of breathing at each threshold before performing the propulsion trials. On any given propulsion trial, the inspiratory threshold was set at 0, 10, or 19 cm · H_2O. Although respiratory frequency increased significantly during propulsion trials, $F(1, 11) = 7.53$, $p < .05$, there was no interaction with the inspiratory threshold, $F(2, 22) < 1$, indicating that the influence of threshold did not change from nonpropulsion to propulsion cycles. The participants propelled the wheelchair without any restrictions placed on the required velocity or propulsion frequency. The last 4 min of each 5-min trial were recorded at 50 Hz. Trial order was randomized and participants were permitted to rest after each trial for at least 5 min. The experiment lasted for approximately 1 hr.

Results

The percentage of time spent performing a given frequency ratio during the three inspiratory threshold conditions is reported in Table 5. As in Experiments 1 and 2, the number reported is the percentage of cycles (>10%) in the area under each peak. In replication of the results of Experiments 1 and 2, participants preferred propulsion-to-respiratory frequency ratios of 2:1, 3:1, and 4:1. Although it appears that experienced wheelchair users exhibited larger and more variable frequency ratios at the lower thresholds than at the higher thresholds, an ANOVA revealed no significant effects. Respiratory frequency, propulsion frequency, and the ratio of the two did not change significantly as a function of the inspiratory threshold, $F(2, 22) < 1$, $F(2, 22) < 1$, and $F(2, 22) = 1.11$, $p > .05$, respectively. Velocity was not controlled, but it also did not change systematically as a function of the threshold manipulation, $F(2, 22) < 1$. The mean elected velocity (3.65 km/hr) was within the range of velocities performed in Experiment 2. Experienced wheelchair users did not differ from novices in their choice of frequency ratio, $F(1, 11) < 1$, nor did level of expertise interact with inspiratory threshold, $F(2, 22) = 1.58$, $p > .05$. Therefore, it appears that challenging the respiratory subsystem by increasing the inspiratory pressure does not alter the activity of the motor subsystem.

In replication of Experiment 2, the phasing of respiration and propulsion was such that the propulsion cycle systematically preceded inspiration. Relative phase was more positive than in Ex-

Table 5
Percentage of Time Spent Performing a Given Frequency Ratio by Experienced Wheelchair Users and Novices for the Three Inspiratory Thresholds in Experiment 3

Inspiratory threshold (cm · H_2O)	Ratio					
	2:1	3:1	4:1	5:1	5:2	Total
Experienced						
0	—	10	28	11	16	65
10	23	32	11	—	—	66
19	20	38	—	—	—	58
Novice						
0	33	10	19	—	—	62
10	36	10	—	—	—	46
19	22	—	40	—	—	62

Note. Dashes indicate a percentage of less than 10.

periment 2 ($M = 26°$), perhaps because the threshold IMT delayed inspiration through its increased pressure requirement. Nevertheless, manipulations of inspiratory threshold did not cause relative phase to shift significantly around this higher mean, $F(2, 22) < 1$. In replication of Experiment 2, there were no effects of level of expertise on relative phase, $F(1, 11) < 1$.

Discussion

In Experiment 2, alterations to the frequency of propulsion produced a change in respiratory frequency and in the ratio between propulsion and respiratory frequency. In the present experiment, inspiratory resistance was manipulated to determine whether challenges to the respiratory subsystem would produce alterations both to the movement pattern, which was not controlled explicitly, and to the coupling of propulsion and respiration. Results showed that manipulations of respiration in terms of inspiratory pressure requirements produced no observable change to respiratory frequency, propulsion frequency, or the ratio of the two. LRC was observed in frequency ratios of 2:1, 3:1, 4:1, 5:1, and 5:2, most of which had been observed in Experiment 1. It is likely that the larger range of ratios resulted from the absence of any constraints on movement frequency that were present in Experiment 2. LRC was also evident in the clustering of relative phase relations around 26°. The hypothesis is offered that manipulation of the inspiratory threshold only served to delay inspiration temporally, thereby increasing the normal lag between the propulsion and respiratory cycle. Although the present findings imply that LRC is unidirectional, it is possible that direct manipulation of respiratory frequency, rather than resistance, may affect LRC in the same manner that propulsion frequency, and not rolling resistance, caused a shift in the frequency ratios. The observation that movement frequency may be the most relevant parameter in determining coupling ratios bodes well in drawing comparisons with the motor coordination literature.

General Discussion

Just as humans and animals demonstrate clear preferences for patterns of gait, there are clearly preferences for coordination among the physiological subsystems of the body. In the present set of experiments, coordination of the motor and respiratory systems was observed in maintenance of small-integer frequency ratios (e.g., 2:1, 3:1, 4:1, and 5:2) and in the consistent placement of the inspiratory phase of the respiratory cycle just after the onset of the propulsion cycle. It is not surprising that there should exist preferences for coordinating the activities of the physiological subsystems of the body. Horses have been shown to walk, trot, and gallop most often at the velocities that minimize oxygen consumption (Hoyt & Taylor, 1981). In humans, oxygen consumption is minimized when rhythmic movements, like bicycling and respiration, are synchronized (Bernasconi & Kohl, 1993). LRC, therefore, may be the body's solution to maximizing its use of resources during challenging aerobic activities. The finding that LRC exists in both lower- and upper-limb exercise confirms the existence of coordination between the physiological subsystems of the body. The next step is to investigate similarities between LRC and the motor coordination literature to determine whether there is a common basis for modeling.

In Experiment 2, increasing the movement frequency led to transitions between frequency ratios, a phenomenon that is common in motor coordination (e.g., Peper et al., 1995a). Unlike the transitions commonly observed in multifrequency coordination, frequency ratios increased—from smaller- to larger-integer ratios—as a function of increased movement frequency. The fact that the transition path was predicted by the Farey tree suggests that the modeling structure may be useful. However, the difference in direction suggests that alterations to coupling strength are somehow different for coordination within and between physiological subsystems. Further investigation of transition direction and pathways is clearly warranted. In the present experiment, it is likely that coupling was unintentional. Testing the intentional maintenance of certain frequency ratios will allow for an assessment of their relative stability. Manipulations of experience may provide an additional index of difficulty if some patterns are stabilized only after training. Finally, scaling the movement frequency within a trial (i.e., using a phase-transition paradigm) would provide a direct test of the Farey tree pathways and a more appropriate comparison to the motor coordination literature.

Coupling is asymmetric in bimanual coordination tasks, as evidenced by greater influence of the preferred hand on the nonpreferred hand than in the opposite direction (e.g., Treffner & Turvey, 1996). When coordination is between the motor and respiratory systems, coupling is also asymmetric, or unidirectional. The results of the present study demonstrate that although the coupling may be mechanically based, it need not be exclusive to influences in the vertical direction. The finding that propulsion frequency (not power output) influenced frequency ratios identifies timing as a critical dimension. In the future, a direct manipulation of respiratory frequency (rather than resistance) may be used to test the hypothesis that only direct variations of a component frequency may bring about alterations to the frequency ratio. The absence of an effect will solidify the claim that LRC is based on unidirectional influence.

There is evidence that different forms of coupling have the same behavioral consequences for two-limb coordination (e.g., Amazeen et al., 1995; Schmidt et al., 1990; Treffner, 1999). In one study in particular, transitions among multifrequency ratios in two-person coordination (coupled acoustically, haptically, or visually) were shown to abide by the same Farey tree principles that accommodate multifrequency coordination within a single individual (Treffner, 1999). Although LRC was investigated in the present study, it is likely that coupling may exist between the motor subsystem and other physiological subsystems that support it, like the cardiovascular system. Cardiac–locomotor coupling has been demonstrated in lower-limb activities (e.g., Kirby, Nugent, Marlow, MacLeod, & Marble, 1989) but has not yet been tested in any upper-limb activities. Investigation of coupling across different physiological subsystems will strengthen the understanding of both the coupling source and coupling behavior during transitions, which may or may not be the same for different pairs of subsystems. Support for general use of the Farey tree to make predictions about coordination both within a single physiological subsystem and between subsystems would allow for a statement of coupling behavior that is independent of the particular coupling medium.

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Received January 18, 2000
Revision received January 16, 2001
Accepted January 22, 2001 ■