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Sound-induced stabilization of breathing and moving

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In humans and other animals, the locomotor and respiratory systems are coupled together through mechanical, neurophysiological, and informational interactions. At a macroscopic observer–environment level, these three types of interactions produce locomotor–respiratory coupling (LRC), whose dynamics are evaluated in this paper. A formal analysis of LRC is presented, exploiting tools from synchronization theories and nonlinear dynamics. The results of two recent studies, in which participants were instructed to cycle or exhale at a natural frequency or in synchrony with an external rhythmic sound, are discussed. The metronome was either absent or present (study 1) and close to or far from the natural frequency of the cycling and breathing systems (study 2). The results evidenced a stabilization of cycling, breathing, and LRC when sound was present compared to when it was absent. A decrease in oxygen consumption was also observed, accompanying the increase in sound-induced LRC stabilization. These results obtained with a simple rhythmic metronome beat have consequences for exercising while listening to music; the consequences are further explored here.

Keywords: locomotor–respiratory coupling; sound; music; efficiency

Locomotor–respiratory coupling

In humans and other animals, the locomotor system and the respiratory system are naturally coupled together, and this coupling is known as locomotor–respiratory coupling (LRC). LRC results from the necessity of the body to fuel muscles with the chemical energy that they need through respiration, bringing oxygen (O_2) into the organism. In the last decade, LRC has been occasionally documented in various forms of rhythmic exercises such as walking,[1,2] cycling,[3] running,[4] rowing,[5] and also during wheelchair propulsion.[6] In most of these studies, entrainment between respiration and locomotion has been described by stable frequency-mode locking patterns—the ratio of breathing cycles over locomotion cycles—such as the ones reported in humans: 1:1, 1:2, 2:3, or 1:4. The existence of LRC and of its various regimes is, however, not confined to humans. Other species such as fish, birds, and quadrupeds have been found to exhibit a similar type of interaction—but with a smaller range of frequency ratios. For instance, quadrupeds most of the time synchronize locomotor and respiratory cycles at a constant ratio of 1:1 (one stride per breath) in both trot and gallop.[7]

The origin of stable LRC frequency ratios (typically 1:1, 1:2, or 1:4) is still unclear today and involves mechanical and neurophysiological factors. From a mechanical point of view, the entrainment of the respiratory system by the locomotor system results from the impact loading on the thorax as the limbs hit the ground—a phenomenon called the visceral piston—from the use of common respiratory and locomotor muscles (e.g., abdominal muscles), as well as from body acceleration and deceleration in horizontal and vertical planes.[7,8] The visceral piston is mostly active during walking and running, in which the mechanical contribution of locomotion to tidal volume approximates 2% in humans.[8] In animals, neurological factors have been offered as a complementary origin of LRC,[9,10] characterized

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by a common control for respiration and locomotion at both cortical[11] and medullar levels.[12] Furthermore, movement-based sensory afferents have been shown to inform respiratory centers in the medulla,[13] including simple rhythmic peripheral tactile stimulation.[14] This neuromotor modulation of respiration is, however, still to be confirmed in humans.

These mechanical and neurophysiological interactions operating during rhythmic movements are constituents of more generic perception–action coupling principles that involve informational parameters. During human walking, for instance, the optical flow created by locomotion can be decomposed into two components, a continuous linear or curvilinear component generated by forward motion[15] and an oscillatory component generated by head motion in the three spatial dimensions.[16] This oscillatory component has been shown to contain relevant information used by humans and other animals[17] to control body sway during walking, based on the congruency between optical motion parallax and expansion/contraction patterns[18,19] and between optical and nonoptical congruencies, for instance through the cyclic stimulation of the vestibular system.[20] Rhythmic locomotion thus produces rhythmic optical consequences at the observation point, which in turn are used to regulate balance during walking. Walking and running also have acoustic and proprioceptive consequences, for instance through the sound produced by the impact of our feet on the ground,[21] by our respiration,[22] as well as through bone conduction.[23]

These self-generated acoustical, optical, and inertial consequences of rhythmic locomotion are not to be underestimated. During a representative walking day, for instance, healthy adults produce around 10,000 steps[24,25] accompanied by the same number of breathing cycles and rhythmic vestibular responses. Although they can create the potential risk of not discriminating self-generated information from critical information in the environment,[26] these perception–action synergies also create opportunities for movement adaptation, perceptual regulation, and efficient behavior in general.

Sound-induced stabilization of LRC at the preferred frequency

External information (such as rhythmic auditory stimulation, RAS) is known to stabilize these natural perception–action synergies. For tapping, the synchronization of movement to a periodic auditory rhythm during bimanual coordination has been shown to enhance motor stability,[27,28] a phenomenon known as the anchoring effect.[29] RAS stabilizes both in-phase and antiphase coordination between the two hands and can postpone the natural transition from antiphase to in-phase when movement frequency increases.[27,28] For breathing, a similar stabilizing effect was found on respiratory frequency when participants passively listened to a periodic metronome or tapped along with it,[30] suggesting a sound-induced stabilization of the respiratory frequency.

In the LRC domain, we have recently conducted a series of experiments testing the stabilizing effect of external auditory information.[31,32] Inspired by pioneering work in the area,[4,33] we have applied a rigorous analysis of LRC, exploiting principles of nonlinear coupled oscillator dynamics, through a generalized version of the sine-circle map model.[34,35] When two oscillators with different eigenfrequencies are coupled, their interactions result in most cases in attraction to a certain frequency ratio, which depends on the ratio between the eigenfrequencies of the two systems (detuning factor) and the strength of the coupling between them. Regions of synchronization and their stability thus depend on the force of the coupling between respiration and locomotion (Fig. 1), emerging from the local interactions among the mechanical, neurophysiological, and informational components reviewed above. In our research, externally generated sound is treated as a coordinating device, and its stabilizing effect on locomotion, respiration, and their coupling is evaluated rigorously.

In a first experiment,[31] healthy adult participants ($n = 16$) were instructed during a cycling exercise to synchronize either their respiration or their pedaling rate with an external auditory stimulus, whose rhythm corresponded, respectively, to their individual preferential breathing or cycling frequencies. The experiment involved four sessions over 2 weeks, including a maximal incremental exercise in order to determine the individual power output at the anaerobic threshold (PAT; session 1), a 10-min exercise at PAT in order to determine individual preferred respiratory and locomotor frequencies (session 2), and sound-paced (sound on or off) cycling or breathing exercises with

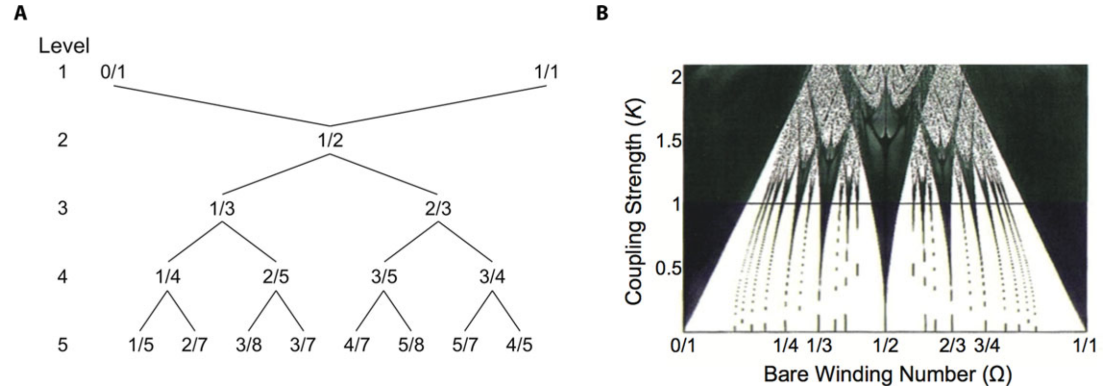

Figure 1. Farey tree and Arnold tongues, two representations of synchronization regions when biological rhythms are coupled. (A) Five first levels of the Farey tree, a hierarchical mathematical structure representing the different frequency ratios of any rhythmic systems coupled together, such as running and breathing, according to their relative stability. Upper-level frequency ratios (e.g., 1:2) are more stable than lower-level ratios (e.g., 3:8); (B) Arnold tongues. Specific mode-locking patterns occur according to the coupling strength (K) and the detuning between the two oscillators (bare winding number). Darker regions correspond to more stable behaviors. Taken from Ref. 31.

specific instructions to cycle or breathe in synchrony with the regular metronome when sound was on (sessions 3 and 4). The main relevant dependent variables included the modal value of the LRC frequency ratio (FRmode), the phase-coupling index (PC), expressing strength of the coupling between the two systems, and the energy efficiency expressed by VO_2. A stabilizing effect of sound on respiration and locomotion was expected in the form of an increase in the occurrence of FRmode, an increase in PC, accompanied by a decrease in VO_2. Statistical significance was tested using an analysis of variance (ANOVA, $P < 0.05$). The results confirmed our predictions. When participants were instructed to breathe or cycle in synchrony with a sound, FRmode increased from 55% to 70%, and PC increased from 11% to 14%. These changes were accompanied by a small but significant decrease in VO_2, from 2.36 to 2.32 L/minute. Interestingly, the effect of sound on LRC happened to depend on the initial LRC stability. Sound stabilized (Fig. 2, left) an initially unstable LRC, while it destabilized (Fig. 2, right) an initially stable LRC. This relation between initial LRC stability and sound-induced (de)stabilization was further quantified by a negative linear correlation (mean r across conditions $= -0.75$) between FRmode in the sound-off condition and the difference in FRmode between both sound conditions (sound-on and sound-off).

Sound-induced (de)stabilization of LRC at an unpreferred frequency

Following this first study, we more recently examined whether the stabilizing effect of a metronome sound is dependent on the rhythm frequency (or tempo) of the presented stimuli. On the basis of results on bimanual coordination and our own results described earlier, we hypothesized that the stabilizing effect of a metronome sound would be maintained at rhythm frequencies far off the preferential respiratory or cycling rhythm frequency (i.e., above and below) compared to silence. In this ongoing work,[32] participants ($N = 15$) again cycled or breathed in synchrony with the external metronome. This time, however, the imposed metronome tempo frequency was -15% (i.e., slow condition), 0% (i.e., preferential condition), or $+15\%$ (i.e., fast condition) of the natural cycling frequency, or -10%, 0%, and $+10\%$ of the natural breathing frequency. In general, the results of this second study were in line with the predictions. Participants were found to increase FRmode (from 41% to 68%) with sound, again providing evidence that periodic auditory stimulation is an efficient way to stabilize the coordination between locomotion and respiration. In addition, the most stable LRC (evidenced by phase-coupling and frequency-coupling indexes) occurred at a preferred frequency, with an increase in variability occurring below or above

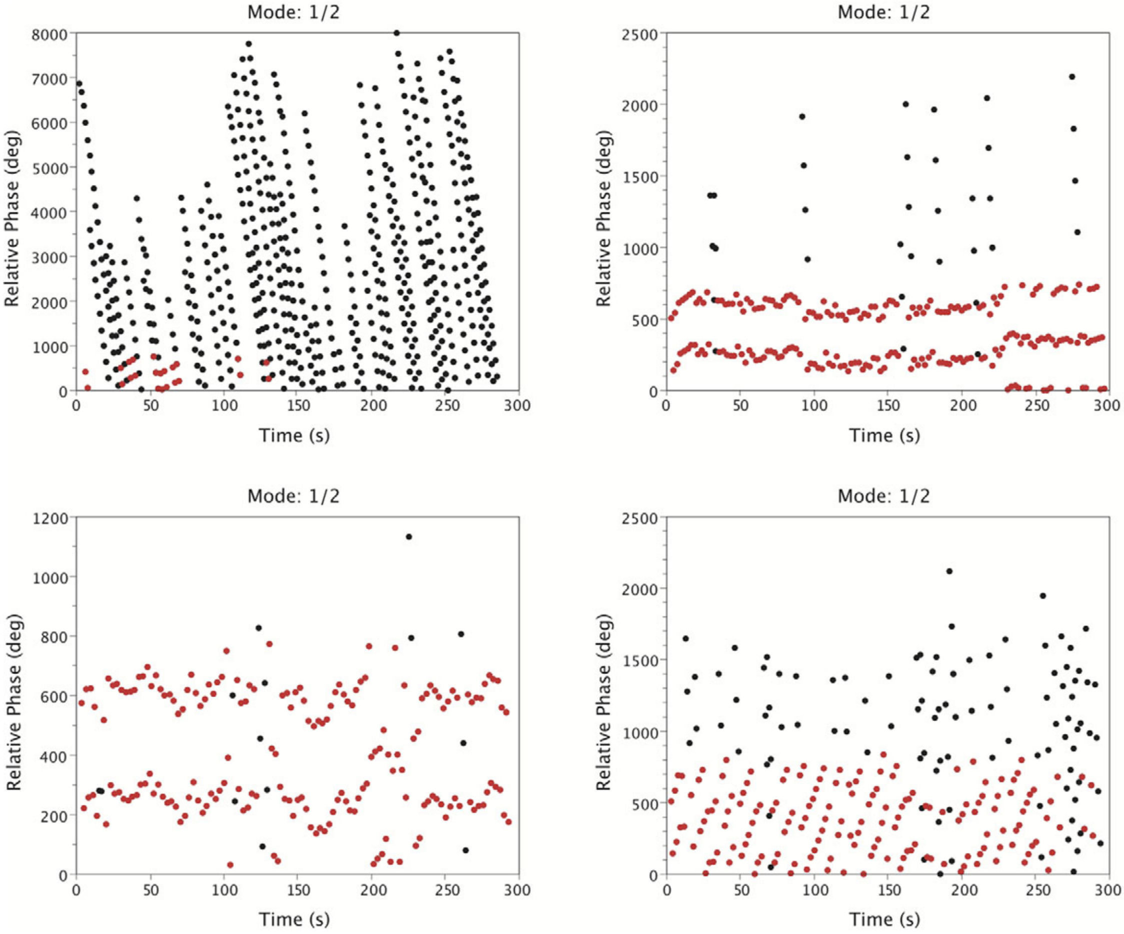

Figure 2. Relative phase series (3 min) between breathing and cycling for two representative participants (left and right), with no sound (top) or under the instruction to breath in sync with the sound (bottom). Red dots represent the relative phase values for the modal frequency ratio, and black dots represent the relative phase values for the other expressed frequency ratios. Adapted from Ref. 31.

the preferred frequency. The silence condition produced the least stable LRC. Figure 3 summarizes the main results.

The results of this second experiment thus confirmed the assumption, both for frequency-coupling and PC indices, that the adoption of locomotor or respiratory preferred rhythms is related to the optimal stability of LRC. Any deviation (i.e., decrease or increase) from preferential frequencies led to a decrease in the coupling strength between the two systems. Also interesting in this study is the finding that the sound-induced stabilization of LRC affected the dynamics of FRmode in the Farey tree described in Figure 1. For instance, by comparing silence with sound conditions, we found that participants used the same modal frequency coupling in about half of the time (46%) but also moved to lower-order ratios (31%) and to higher-order ratios (23%) in the presence of the metronome. Furthermore, these changes in FRmode frequently led to an increase in LRC stability with larger benefits when displacements in the Farey tree occurred from higher-order ratios to lower-order ratios.

This result suggests that the increase in LRC stability with sound was a combined effect of (1) an intrinsic sound-induced stabilization of FRmode and (2) the adoption of more stable frequency ratios in the Farey tree. Similar comparisons between the preferential condition and the two other sound conditions revealed a decrease in LRC values for participants using the same FRmode across conditions. This suggests a destabilizing

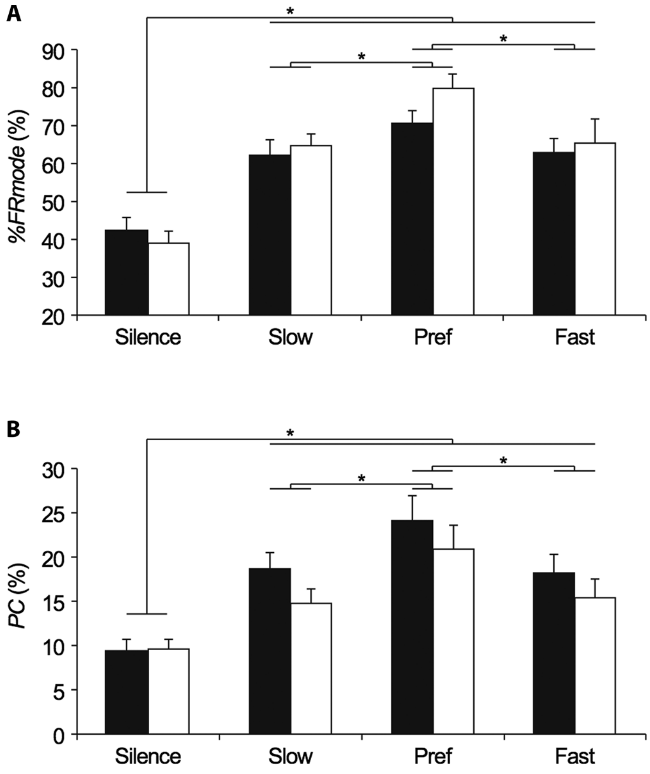

Figure 3. Mean occurrence of (a) the modal frequency ratio (%FRmode) and (b) the phase-coupling index (PC) when participants were instructed to cycle (black bar) or to breathe (white bar) in sync with the metronome pacing at different frequencies. Error bars represent standard errors. $^*P < 0.05$. Adapted from Ref. 32.

effect of nonpreferred frequencies on LRC. Together, these results indicate that lower values of LRC in slow and fast conditions resulted from the synchronization with nonpreferred sound frequencies, associated with more displacements toward less stable frequency ratios than toward more stable ratios (see Ref. 31 for further details).

The role of music in stabilizing LRC

The results reported above confirmed that simple periodic auditory stimulation is an efficient way to stabilize LRC. We can question whether the same holds for LRC in the presence of a richer auditory stimulus, such as music, which is composed of multiple embedded periodicities and has complementary ergogenic effects. For instance, the musical beat is well known to entrain body movements.[36,37] This entrainment is natural, universal, and probably hard-wired in humans.[38] The power of music to entrain biological rhythms (e.g., walking or running) is not confined to movement. The respiratory rhythm is also captured by a musical beat during passive listening.[30,39] The action of music on biological rhythms is likely to be underpinned by a rhythm-driven sensorimotor network particularly recruited by musical beat, which includes perceptual (e.g., the superior temporal gyrus), motor (e.g., motor cortex), and sensorimotor integration areas (e.g., premotor cortex) as well as subcortical structures such as the basal ganglia and the cerebellum.[40–43] It is conceivable that music, through its coordinating role on LRC, contributes to a larger diminution in oxygen consumption as compared to a simpler rhythmic auditory sequence, such as that produced by a metronome. One currently tested direction is the manipulation of the characteristics of the auditory stimulus presented to the participants in similar experiments. Preliminary results suggest that running to the beat of music increases FRmode and the PC index in addition to boosting energy efficiency.[44]

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Conflicts of interest

The authors declare no conflicts of interest.

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