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## Why do we move to the beat? A multi-scale approach, from physical principles to brain dynamics

Loic Damm, Déborah Varoqui, Valérie Cochen de Cock, Simone Dalla Bella,  
Benoît Bardy

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1 **Why do we move to the beat? A multi-scale approach, from**  
2 **physical principles to brain dynamics**

3

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24

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1

## **Abstract**

2 Humans' ability to synchronize movement with auditory rhythms relies on motor  
3 networks, such as cortical areas, basal ganglia and the cerebellum, which also  
4 participate in rhythm perception and movement production. Current research has  
5 provided insights into the dependence of this action-perception coupling upon the  
6 entrainment of neuronal activity by external rhythms. At a physical level, advances  
7 on wearable robotics have enriched our understanding of the dynamical  
8 properties of the locomotor system showing evidences of mechanical  
9 entrainment. Here we defend the view that modelling brain and locomotor  
10 oscillatory activities as dynamical systems, at both neural and physical levels,  
11 provides a unified theoretical framework for the understanding of externally  
12 driven rhythmic entrainment of biological systems. To better understand the  
13 underlying mechanisms of this multi-level entrainment during locomotion, we  
14 review in a common framework the core questions related to the dynamic  
15 properties of biological oscillators and the neural bases of auditory-motor  
16 synchronization. Illustrations of our approach, using personalized auditory  
17 stimulation, to gait rehabilitation in Parkinson disease and to manipulation of  
18 runners' kinematics are presented.

19

20

## **Key Words**

21

22 Rhythm, synchronization, music, auditory cueing, walking, running, cadence,  
23 dynamical systems, oscillators, beat, prediction

24

25

## Highlights

1

2 • What does lie behind the ergogenic benefit of music?

3

4 • Locomotion and a large number of natural movements consist of neuronal and  
5 mechanical oscillations.

6

7 • Evidences exist that predictable beat-based auditory stimulations entrain  
8 neuronal activity and engage the motor structures of the brain.

9

10 • Modelling external and internal rhythms as oscillators provides a unified  
11 theoretical framework in which sensory and motor structures are bound to each  
12 other during auditory motor synchronization.

13

14 • Neural mechanisms associated with beat tracking ability support gait  
15 rehabilitation of Parkinson's disease patients and contribute to stabilize spatio-  
16 temporal gait parameters of runners.

17

18 • Exogenous rhythms, in order to entrain locomotion, need to comply with specific  
19 properties of biological oscillators, at neural as well as physical levels.

20

21

22

## 1           **1    Introduction**

2           Auditory rhythms are a strong movement incentive. The potential of music  
3 as a driving force for movement translates into the ubiquitous human tendency to  
4 move to the beat (Repp, 2005), the most salient rhythmical event. In daily life,  
5 people spontaneously or deliberately move to the beat of rhythmic sound  
6 sequences via finger or foot tapping, body swaying or walking (Leman et al., 2013).  
7 This ability, which appears to be natural and universal, develops early in  
8 humans (Zentner & Eerola, 2010). What lies behind this ergogenic benefit of  
9 music? The coupling between perception and action contributes to the  
10 emergence of the compelling link between rhythm and movement. A growing  
11 body of evidence shows that merely listening to a musical beat activates motor  
12 regions of the brain (Grahn & Rowe, 2009; Zatorre et al., 2007). Due to its peculiar  
13 and unique rhythmic features - i.e. a regular and prominent beat structure (Fitch,  
14 2013) - music is thus ideally suited to drive the motor system (Dalla Bella et al.,  
15 2013; Madison, 2014).

16

17           In this article, we propose to analyse the ability of music to entrain  
18 movement, and we do so by reviewing experimental and modelling evidences of  
19 its physical and neuronal underpinnings. A particularly targeted context is human  
20 locomotion, e.g. walking and running. If virtually any rhythmical movement can be  
21 guided by an external rhythm, the intrinsic rhythmicity of locomotion indeed  
22 makes it a relevant target. Some structures, such as central pattern generators,  
23 have been phylogenetically selected to generate locomotor rhythms (Guertin,  
24 2012). Among the hard-wired factors contributing to gait rhythmicity, some are  
25 specific to human lineage and relate to our proficiency in walking and running  
26 (Bramble & Lieberman, 2004). The relative extension of leg joints, typical of  
27 human gait, makes the maintenance of locomotor cycles possible at a low  
28 energetic cost (Sockol et al., 2007) despite the inertia of the lower limb. The widely

1 accepted mechanical models of walking and running, i.e. the inverted pendulum  
2 system (Cavagna et al., 1963; Cavagna & Margaria, 1966) and the mass spring  
3 system (Cavagna et al., 1964; Alexander, 1988; Blickhan, 1989) respectively  
4 (Cavagna et al., 1977), account for the execution of these periodic motions.  
5 Biological oscillators successfully combine energy dissipation and injection, i.e.  
6 damping and actuation exerted by the muscles (Gurfinkel et al., 1998;  
7 Gerasimenko et al., 2010), to ensure the robustness of their trajectories  
8 (Hurmuzlu & Moskowitz, 1986). These complementary mechanisms ensure gait  
9 stability. Being stable means that the rejection of perturbation is a core capability  
10 of the system. However, real time manipulation of the dynamical environment  
11 during walking demonstrates the possibility to mechanically entrain gait patterns  
12 (Ahn & Hogan, 2012b). In other words, despite gait steadiness, interactions with  
13 external rhythmical events are possible, and contribute to the stabilizing or  
14 destabilizing of walking and running.

15

16 Locomotion does not rely on simple mechanics. If the possibility to entrain gait  
17 with auditory rhythms exists, it requires the engagement of supervising  
18 structures. During finger tapping, imagery studies have revealed the contribution  
19 of motor structures of the brain during the extraction of an auditory rhythm, e.g.  
20 the pulse underlying a temporal pattern (Zatorre et al., 2007; Bengtsson et al.,  
21 2009; Grahn, 2012; Chen et al., 2006; Chen et al., 2008a). Contrasting auditory-  
22 paced movement vs. self-paced dance steps (Brown et al., 2006) showed  
23 activations specifically related to beat information during bipedal movements.  
24 Sustained periodic cortical response tuned to the frequency of auditory rhythms,  
25 as shown in electroencephalographic (EEG) studies (Nozaradan et al., 2011), can  
26 be interpreted as a manifestation of cortical entrainment. It has been suggested  
27 that oscillations, which are naturally observed both at cellular and neuronal levels,  
28 contribute to the central representation of event timing (Large et al., 2015). In  
29 more dynamical terms, an appealing theoretical model consists in viewing



1 neurodynamics as the support of auditory rhythm perception, and its corollary,  
2 motor synchronization.

3

4 In this contribution, we propose that sound-induced locomotor entrainment is  
5 distributed throughout interacting and reciprocally influencing neural and physical  
6 levels of behaviour. Furthermore, we argue that this multi-level entrainment  
7 organization promotes auditory-motor synchronization (AMS) as a factor of motor  
8 performance. Appropriate spatio-temporal activation of muscles is necessary for  
9 movement production, and auditory afferences can positively influence the  
10 temporal structure of motor activities when they match the requirements of the  
11 task and the intrinsic properties of neurophysiological and biomechanical  
12 oscillators. Multiple interconnected biological oscillators, although different in  
13 their structure, can be entrained to the same external rhythm. Despite the  
14 singularities of brain structures (governed by neurophysiological principles) and  
15 locomotor structures (obeying mechanical laws), modelling both structures as  
16 (coupled) dynamical systems provides one unifying functioning principle. From  
17 perception to action and from action to perception, tracking the influence of  
18 external rhythms onto biological rhythms can enable a better understanding of  
19 how rhythmical auditory stimulations find their way to motor commands and  
20 movement control, and can benefit from our multi-level entrainment framework.

21

22 Specifically, the main goal of the present review is to show how the interplay  
23 between neuronal, physiological and biomechanical mechanisms can generate  
24 the behavioural findings reported in the literature, and affect performance.  
25 Because AMS blends physical and neural processes, the boundaries of the present  
26 review span across disciplines beyond the strict scope of neuroscience. In the next  
27 sections, we introduce the theoretical framework of entrainment and then  
28 explore its ramification at biomechanical, physiological and neurophysiological  
29 levels. We detail how the chain of oscillators at these different levels are prone to

1 entrainment during locomotor activities, and how AMS can contribute to the  
2 timing of action and associated performance. The use of AMS for the gait  
3 rehabilitation of PD patients and for entraining runners' cadence will provide  
4 examples of the potential benefits of AMS delivered during locomotion. These  
5 applications will finally feed the research agenda that we propose for future work  
6 in this fast-changing area of research.

## 7           **2 Rhythmic Movement and auditory-motor** 8           **synchronization as Coupled Oscillators: the** 9           **Dynamical Systems Approach**

10 The dynamical systems theory provides a framework to model movement  
11 characteristics in the context of AMS. Moving in synchrony with an external  
12 rhythm (a metronome or music) implies that predictable auditory events pace the  
13 movement. The beat corresponds to the regular time interval that we can tap  
14 along to when listening to music (Cooper & Meyer, 1960; Large, 2008). It  
15 corresponds to an internal pulse resulting from the temporal organization of  
16 durations in the musical piece, including different embedded periodicities (metre;  
17 London, 2012). Whereas metronomic ticks provide unambiguous temporal cues,  
18 in a musical stream, the beat is not necessarily a strict property of the stimulus.  
19 Due to the complexity of musical structure, the possibility to interpret multiple  
20 periodicities often exists. Beats being "inferred from but not identical to the  
21 patterns of accentuation at the musical surface" (Lerdahl & Jackendoff, 1983),  
22 variations of acoustic parameters such as pitch (Prince et al., 2009; Ellis & Jones,  
23 2009; Prince, 2014) or intensity (Drake et al., 2000b) can also contribute to beat  
24 perception. The metrical hierarchy can modulate the saliency of some beats with  
25 respect to others, every other beat being accented, e.g. in a march rhythm.  
26 Studying the temporal alignment of actions related to these auditory landmarks  
27 has enabled the investigation of AMS.

1

2 Rhythmic movements - such as those occurring during tapping or locomotion -  
3 provide the moving limb(s) with the properties of a self-sustained oscillator,  
4 characterized by a natural frequency, i.e. the frequency of the system measured  
5 when isolated, not determined by the initial conditions at movement onset but by  
6 its internal properties, with the ability to be restored after a transient  
7 perturbation. Synchronization occurs when two oscillators adjust their rhythms by  
8 virtue of their interaction. The nature of the interaction can be of different origin:  
9 the synchronization of two clocks hanging from a common support observed by  
10 Huygens (Huygens, 1665) is a famous example of mechanical coupling. How weak  
11 or strong the interaction indicates that coupling strength is not easy to measure  
12 (Pikovsky et al., 2003). In the case of Huygens' clocks, it depends on the ability of  
13 the board supporting the clocks to move, coupling strength being the first factor  
14 affecting the synchronization of two oscillators. The second factor is the frequency  
15 detuning, which refers to the distance between the preferred frequency of the  
16 two oscillators. When the distance between the two natural frequencies is large,  
17 their interaction does not result in the establishment of a common oscillation  
18 frequency. On the contrary, for a certain range of detuning, which delimits a  
19 synchronization region, the frequency of each oscillator is entrained towards an  
20 equal frequency, and synchronization occurs. The width of the synchronization  
21 region in frequency relates to coupling strength and detuning: the wider the  
22 region, the stronger the coupling.

23

24 When oscillation frequencies lie within the synchronization boundaries and the  
25 coupling between oscillators is strong enough, the oscillators' frequencies  
26 converge to the same value, i.e. are entrained, and synchronization occurs.  
27 However, by looking at the phase of each oscillator, defined as their instantaneous  
28 position on the waveform cycle, different synchronization regimes can be  
29 distinguished. In agreement with the description of frequency entrainment or

1 frequency locking between oscillators, von Holst (1973), observing the  
2 coordination of fish fins, emphasized the contribution of two properties of  
3 neuronal oscillators. The *beharrungstendenz*, or maintenance tendency, describes  
4 the steadiness of oscillations, whereas the *magneteffekt*, or magnet effect,  
5 accounts for the influence that one oscillator can exert onto another one differing  
6 by its eigenfrequency, resulting in the progressive drawing and coupling to its own  
7 frequency. Both effects are in competition and contribute to relative coordination.  
8 Von Holst interpreted fins moving at the same frequency with a constant phase  
9 relation as the dominance of the second effect. The distinction between  
10 synchronization regimes thus benefits from the measure of the relative phase,  
11 defined as the phase difference between the two oscillators.

12

13 Having introduced the properties of oscillatory systems, we can now outline the  
14 reasons why the coupled-oscillators model has been proposed as a model of  
15 auditory-motor synchronization. It involves an adjustment of the motor rhythm to  
16 ensure synchronization with the tempo of external sensory events. This is why  
17 tempo has been considered as one of the most significant determinants of AMS-  
18 related effects on rhythmic movements. Coupling strength can be measured by  
19 the ability of the participant to reach and maintain his/her movements in  
20 synchrony with the beats of the auditory stimulation. When the frequency of  
21 external stimulations is fixed, coupling is unidirectional. Hence, the auditory beats  
22 are used as a forcing oscillator. When movement frequency is entrained to the  
23 frequency of auditory stimulations, the moving limb often oscillates at the  
24 externally driven tempo, as long as the detuning is not too pronounced, giving rise  
25 to frequency locking. In-phase synchronization (equivalent to absolute  
26 coordination reported by von Holst, 1973) occurs when both oscillators reach the  
27 same extreme positions simultaneously (the rightmost or leftmost positions in the  
28 case of two pendulums, tapping on the beat in the case of auditory tapping)  
29 whereas anti-phase synchronization (one specific case of relative coordination) is

1 characterized by movements in the opposite direction of each oscillator (one  
2 pendulum being in the rightmost position when the other one is in the leftmost  
3 position or tapping at half the period of the auditory stimulus, which results in  
4 syncopation instead of synchronization). Entrainment is the process through  
5 which two oscillators are attracted to each other by virtue of their interactions.  
6 The term entrainment is often used to refer not only to the case of perfect period  
7 and phase synchronization, but also to the tendency towards that state, perfect  
8 synchronization being just one specific case of entrainment (Troost et al., 2017).  
9 Studying sensorimotor synchronization therefore consists in characterizing  
10 frequency and phase anchoring between movement cycles and auditory stimuli.

11

12 An appropriate tempo of auditory stimulation is not sufficient to ensure  
13 sensorimotor synchronization. Since rhythmical voluntary movements involve  
14 bringing the effector into a specific position at a specific time, movement phase  
15 coordination with external sensorimotor events is required to ensure their  
16 representativeness in time and space. Plotting movement kinematics in a state  
17 space such as the space of flexion-extension angles of opposite lower limb joints  
18 makes the invariance visible in coordination patterns. A specific form of the state  
19 space - the phase portrait - where the angle and angular velocity of an oscillatory  
20 system are plotted against each other reveals the presence of attractors (Beek,  
21 1989), which correspond to the regions where the dynamics tend to converge  
22 onto a relatively limited number of values. In other words, attractors are  
23 characterized by the reduction of the spatio-temporal variability (Byblow et al.,  
24 1994; Fink et al., 2000; Maslovat et al., 2009). The influence of auditory-motor  
25 synchronization on their emergence (Byblow et al., 1994; Fink et al., 2000)  
26 ascertains the contribution of auditory input to motor coordination, and is visible  
27 in the phase portrait as the rapid convergence towards the aforementioned  
28 values. This influence legitimates the modelling of the motor system and

1   rhythmical auditory stimulations as coupled oscillators, a theoretical framework  
2   in which the coordination of the former can be governed by the latter.

### 3           **2.1    Attractors Determine Global Movement Dynamics and Affect** 4           **AMS Stability**

5   In the dynamical approach, the control of motor timing by central structures is  
6   considered as an emergent property of dynamical movement principles (Yue et  
7   al., 2000; Kelso, 1995; Turvey, 1990) as opposed to the information processing  
8   theory which postulates the existence of a central timekeeper (cf. box 1, section  
9   7.1). Support to the dynamical systems approach can be found in the kinematic  
10   structure of rhythmic movements.

11

12   As presented in the above paragraph, sensorimotor synchronization is  
13   characterized by phase and frequency matching between external stimulations  
14   and movement. The former ensures timing accuracy when the latter yields  
15   appropriate time intervals. By varying the frequency of bilateral index finger  
16   oscillations, considered as a representation of coordinated movements, Kelso et  
17   al. (1981) revealed two stable modes of bimanual coordination: (i) the *in-phase*  
18   pattern where the relative phase between each finger's position is zero, and (ii)  
19   the *anti-phase* pattern characterized by a  $\pm \pi$  relative phase. These patterns can  
20   be mapped onto point attractors. Haken et al. (1985) proposed a dynamical model  
21   accounting for the observed phase diagram. In the Haken-Kelso-Bunz (HKB)  
22   model, the relevant control parameter is the frequency of oscillations (Schöner &  
23   Kelso, 1988).

24

25   Stable convergence to a dual state is not the only behaviour of a damped mass-  
26   spring system. Robustly sustained oscillations having a stable amplitude and  
27   frequency with respect to perturbation can also characterize a second-order  
28   dynamical system exhibiting limit-cycle behaviours, which appears to be a

1 landmark of biological oscillators. Kay et al. (Kay, 1988; Kay et al., 1987)  
2 interpreted rhythmic finger movements as the combination of noise and limit-  
3 cycle dynamics. Fluctuations around a cyclic orbit in the phase plane subsequent  
4 to perturbations ascertain the stability of the limit cycle attractor (Kelso et al.,  
5 1981). In fact, any path in the state space can be considered as an attractor,  
6 contributing to the stability of movement kinematics (Shadmehr & Mussa-Ivaldi,  
7 1994; Won & Hogan, 1995; Burdet et al., 2001). Trajectory robustness and  
8 attractors are tightly linked because the latter ensure the re-emergence of the  
9 former after perturbation. The correspondence between periodic attractors and  
10 rhythmical movement shows that an attractor can act as a deterministic factor of  
11 movement dynamics (Rabinovich et al., 2006). From the study of phase  
12 transitions, i.e. discontinuities in coordinated movements, Haken et al. (1985)  
13 unveiled how the apparent bimodal instability fosters synergies, defined as  
14 “functional groupings of structural elements (e.g. neurons, muscles, joints) that  
15 are temporarily constrained to act as a single coherent unit” (Kelso, 2008).  
16 Identifying synergies sustained by perceptual events can therefore address the  
17 question of movement stabilization by sensorimotor synchronization. The shape  
18 of the limit cycle of cyclical movements can be altered by rhythmical stimulations,  
19 or more exactly by certain properties of the sensorimotor coupling. In addition,  
20 the cognitive intent appears to shape the asymmetry between flexion and  
21 extension phases (Carson & Kelso, 2004). For instance, Wachholder and  
22 Altenberger (1926) (cited in Sternad, 2001) reported during wrist flexion-  
23 extension alternations that the instruction could put the emphasis on one of the  
24 phases. However, flexion-extension alternations of the finger entailed a  
25 systematic accentuation of the flexion phase. Instructions to accentuate the  
26 opposite phase altered the level of coordination. Poor synchronization  
27 performances have also been associated with off-the-beat synchronization  
28 (syncopation) at high tempo (Kelso, 1995), compared to on-the-beat  
29 synchronization. Finally, constraints arising from the neuromuscular properties

1 can also contribute to shaping the phases of synchronized movements. The  
2 frequent transition from an extend-on-the-beat pattern to a flex-on-the-beat one  
3 at high tempo also evidences the influence of the neuroanatomical characteristics  
4 of recruited muscles (Carson & Riek, 1998). As anti-gravity muscles, flexors are  
5 stronger than extensors, require a smaller proportion of motor unit recruitment  
6 for the same force production (Vallbo & Wessberg, 1993), receive more  
7 facilitatory projections from the cortex (Palmer & Ashby, 1992) and require less  
8 cortical activity (Yue et al., 2000). In short, the intention and differential  
9 neuroanatomical organization of flexion and extension, among other factors,  
10 contribute to AMS stability (Carson & Kelso, 2004). A deep understanding of  
11 structural and functional properties of biological effectors is required to catch how  
12 their emergent dynamical properties contribute to a successful auditory-motor  
13 synchronization.

## 14 **2.2 Low-Level Movement Parameters Affect Rhythmic** 15 **Entrainment**

16 Zooming down towards the lower level of movement parameters, such as the  
17 resonant frequency of the end effector and its muscular activities, allows us to  
18 explore the complementary effects of auditory stimulation on movement  
19 production. First, any moving segment is characterized by its eigenfrequency.  
20 Auditory-motor frequency locking occurs when the frequency of the stimulus and  
21 the eigenfrequency of the system under scrutiny are not too far apart (Leman,  
22 2016), or are at multiples (Roerdink et al., 2009) or fractions (Bouvet et al., 2019)  
23 of the natural frequency of the system. When participants perform underarm  
24 swings while keeping in cadence with audio-visual stimuli, better synchronization  
25 accuracy at a preferred tempo (i.e. the tempo spontaneously adopted by  
26 participants, which is at or close to the resonant frequency of the moving limb  
27 (Goodman et al., 2000; Abe & Yamada, 2003)), rather than at a faster or slower  
28 tempo, is usually reported (Smoll & Schutz, 1982). This finding is in agreement with



1 the theory of dynamical systems. It confirms the existence of a basin of  
2 entrainment, resulting in convergence towards the limit cycle, partly determined  
3 by the inertia of the moving limb (Hatsopoulos & Warren Jr, 1996).

4

5 Second, entrainment is also visible at the muscular level. Safranek et al. (1982)  
6 were among the first to relate electromyographic (EMG) activities with auditory  
7 cueing. In their study, participants were instructed to achieve a sequence of  
8 reaching movements between three targets in silence, while listening to even or  
9 uneven rhythms. EMG variability decreased under the influence of even rhythm  
10 while it increased with uneven rhythm. Thaut et al. (1991) noticed less co-  
11 contraction of biceps and triceps during a flexion-extension task of the elbow  
12 eliciting up- and down-swings of the forearm when the tempo of auditory cues  
13 was matching the natural frequency of the movement compared to the same  
14 movement performed in silence. An external rhythmical pacemaker can thus elicit  
15 changes in onset, duration, and variability of muscular activities during simple  
16 flexion-extension movements or during more complex movements such as  
17 reaching. In a more recent study, Yoles-Frenkel et al. (2016) clarified the influence  
18 of auditory context on the kinematics and corresponding patterns of muscular  
19 activity during a finger tapping task. They confirmed the reduction of EMG  
20 variability in response to auditory cues and noticed the concomitant reduction of  
21 variability in the velocity profiles. More specifically, the variability of both  
22 acceleration and muscle activity was reduced when tapping was auditorily cued,  
23 during the pre-tap period, but not during the actual tap. Taken together, these  
24 findings witness auditory entrainment to the beat at the level of the  
25 neuromuscular machinery, from muscular activities to limb movement.

## 2.3 The Contribution of Nonlinear Oscillators to Locomotor Control

An enormous literature, partly cited in the present review, has analysed AMS-related human behaviour during isolated cyclical movements of the upper limb, such as during tapping to the beat, which is not the most representative movement of our everyday life repertoire. In contrast, locomotion, together with the way the two lower limbs have functionally been coupled throughout evolution, has been less studied in the AMS context. Locomotion is probably the most phylogenetically preserved rhythmical physical activity in humans and other animals. Beyond striking differences between species, e.g. quadrupedalism vs. bipedalism, evolutionary conservation has shown similarities in the development of the neural command of locomotion (Grillner, 2011). All vertebrates possess spinal neuronal networks called Central Pattern Generators (CPG), which can produce meaningful functional patterns of motor activities in the absence of sensory inputs (Brown, 1914). CPG activity has been evidenced by fictive locomotion when the spinal cord is isolated from the periphery in non-human vertebrates (Brown, 1911; Grillner & Wallén, 1985; Grillner et al., 1998). In humans, the evocation of locomotor movements with spinal electromagnetic stimulations provides an indirect indication of the presence of CPG in the spinal cord (Gerasimenko et al., 2010). Nonlinear oscillators used to model CPG (Matsuoka, 1987; Collins & Richmond, 1994; Rybak et al., 2006) possess distinctive properties such as stability, that enable input from feedback pathways with a high entrainment potential. Locomotion would be supported by lower-level command modules, possessing the characteristics of nonlinear oscillators, engaged in specific rhythm generation (a configuration which is more unlikely to underlie tapping for example). However, the gait of patients suffering from spinal cord injury also suggests the contributing role of the supraspinal command to locomotion. Indeed, patients following body-weight support training after recovery exhibit a foot trajectory close to that of healthy participants, with a

1 different lower-limb coordination when evaluated through the phase relation of  
2 their angular motion (Grasso et al., 2004).

3

4 High-level and low-level commands are thus not mutually exclusive in producing  
5 entrainment, and their complementary nature has been studied, for instance by  
6 Ahn and Hogan (2012b). In a striking study, the authors attempted to assess their  
7 respective contributions during walking. They used an innovative therapeutic  
8 robot able to mechanically perturb the ankle joint. The command of the robot,  
9 designed as a torsional spring compensating for its intrinsic inertia, applied  
10 periodic mechanical perturbations. Periodic square plantar-flexor torque pulses  
11 were applied at frequencies different to the walker's preferred cadence. This set-  
12 up was designed to test the dynamic entrainment hypothesis. The torque  
13 perturbation was delivered at constant frequency throughout one trial and  
14 consequently the relative phase between its occurrence and gait could vary. The  
15 evolution of relative phase across successive strides after the application of low-  
16 to high-frequency perturbations was used to assess the basin of entrainment.  
17 Walking was found to be entrained by the mechanical perturbation, although only  
18 for a limited range of perturbation frequencies. Phase locking occurred during the  
19 push-off phase such that the perturbation assisted the movement. These  
20 behavioural results, in agreement with the prediction of the nonlinear coupled  
21 oscillators theory, show the possible contribution of neuro-mechanical oscillators  
22 to walking. However, these effects appear to be modest, as witnessed by the slow  
23 convergence of steps and perturbation phases. Ahn and Hogan's (2012b)  
24 conclusion calls for the coexistence of spinal semi-autonomous oscillatory  
25 activities and central supervision, a hierarchical organization they refer to as the  
26 "episodic supervisory control of a semi-autonomic periphery". This engineering  
27 terminology resonates with the functional anatomy of locomotion. CPGs, which  
28 are distributed spinal networks responsible for the sequential activation of  
29 antagonist muscle groups (Grillner, 1981), are not the only subsystems involved in

1 the control of locomotion (Figure 2E). Brainstem command centres activate CPGs,  
2 silent at rest, via reticulospinal neurons, which integrate afferent sensory  
3 feedback (Zehr & Duysens, 2004; Nielsen, 2003) and vestibular signals (Zelenin et  
4 al., 2007). Integration of posture and locomotion is a prerequisite for ensuring  
5 propulsion, but adaptation of the building locomotor blocks to a behavioural  
6 context is also necessary. Experiments in animals have demonstrated the  
7 contribution of the forebrain in movement adaptation (Bjursten et al., 1976;  
8 Whelan, 1996). But the fine-tuning of behavioural repertoire benefits from cortical  
9 input, the fast-direct corticospinal pathway projecting on most human muscles  
10 (Mills, 1999). Interestingly, the direct micro-stimulation of the motor cortex in  
11 autonomous walking animals was found to reset step cycle during stance, whereas  
12 it increased activity level and duration of flexor muscles during the swing phase  
13 (Bretzner & Drew, 2005). The motor cortex thus appears to contribute to both the  
14 structure and the timing of locomotor patterns.

15

16 The functional organization described above raises the question of the possible  
17 influence of periodic auditory stimulations on locomotor activities. A number of  
18 studies have shown the influence of rhythmical auditory cues on spatiotemporal  
19 parameters of gait. Participants instructed to synchronize their footsteps with a  
20 metronome 22.5% faster than their natural cadence increased their walking  
21 velocity by increasing their cadence (Leow et al., 2014). Metronome clicks, when  
22 10% faster than a healthy elderly cadence, have recently been found to elicit the  
23 increase of both stride length and cadence in the Dotov et al. (2019) experiment.  
24 Roerdink et al. (2011) showed that the efficacy of auditory stimulations to elicit  
25 gait changes weakened as a function of the gap between pacing tempo and  
26 participants' cadence, an observation in line with the dynamics of coupled  
27 oscillators. Beat perception has also been found to accompany the modification  
28 noticed in gait performance when synchronizing footsteps with auditory cues. For  
29 instance, Leow et al. (2014) reported an association between strong beat

1 perception and gait performance in the presence of a metronome or music,  
2 whereas weak beat-perceivers exhibited slower, more cautious gait, particularly  
3 in the presence of musical excerpts with non-salient beats. Ready et al. (2019)  
4 confirmed the alteration of gait, as indicated by the increase of double-limb  
5 support time, in weak beat-perceivers instructed to synchronize their steps with  
6 rhythmical cues, either a metronome or low-beat saliency music. From these  
7 converging results, we can conclude that there is an interaction between beat  
8 perception ability and auditory-based gait control, illustrating the circular  
9 causality between perception and action during AMS. We now focus on the neural  
10 processes allowing the brain to make use of the temporal regularities of  
11 rhythmical auditory stimulations during motor activities.

### 12 **3 The Neural Bases of Auditory-Motor Synchronization**

13 In the previous section (2), we clarified the physical principles producing  
14 entrainment according to the dynamical systems perspective, and how they could  
15 contribute to coupling movement characteristics with auditory beats . Considering  
16 the oscillatory nature of locomotor activities, walking and running represent a  
17 natural target for periodic auditory-cueing, which can be achieved only if  
18 information finds its way into the motor system. We have demonstrated various  
19 levels of auditory entrainment, from localized muscular activity to the movement  
20 of one joint, to a more global entrainment of the locomotion system when  
21 external rhythmic auditory events take place. We now focus on the brain  
22 structures involved in that biological entrainment to the beat. Despite our interest  
23 in locomotion, this class of movement does not occupy the largest place in AMS  
24 studies. In particular, the simple task of finger tapping to an auditory sequence of  
25 tones has been a widespread approach in laboratory studies (for a review see  
26 Repp, 2005 and Repp & Su, 2013). This task, which requires moving only one  
27 finger, facilitates the listening of stimuli and the design of experimental set-ups.  
28 The precision of data acquisition from neuroscience methods, particularly brain



1 premotor cortex, supplementary motor area, pre-supplementary motor area,  
2 lateral cerebellum and basal ganglia when participants are listening to beat-based  
3 rhythms (Grahn & Brett, 2007; Chen et al., 2008a; Grahn, 2009; Bengtsson et al.,  
4 2009; Grahn & Rowe, 2009; Grahn & Rowe, 2013; Kung et al., 2013; Merchant et  
5 al., 2015; Chauvigné et al., 2014). The same structures appear to be associated  
6 with beat-driven actions (Rao et al., 1997, Schubotz et al., 2000, Rao et al., 1997,  
7 Dhamala et al., 2003, Lewis et al., 2004, Kung et al., 2013, for a meta-analysis, see  
8 Chauvigné et al., 2014 and Merchant et al., 2015).

### 9           3.1.2    *Movement Sequence Organization in the Motor Cortex*

10 The traditionally accepted functions of premotor (PMC) and supplementary motor  
11 (SMA) cortices include the organization of sensory information relevant for the  
12 guidance of the movement towards the goal (Weinrich & Wise, 1982), and for the  
13 planning of ordered sub-movements, respectively (Mushiake et al., 1991; Tanji &  
14 Shima, 1994; Shima & Tanji, 1998). PMC contributes to the production of  
15 isochronous rhythms but is not specifically related to sensorimotor  
16 synchronization. For instance, during an auditory-paced hand movement, Pollok  
17 et al. (2017) reported the absence of modulation of synchronization accuracy  
18 while stimulating dorsal PMC with transcranial direct current stimulation (tDCS).  
19 In contrast, the pre-supplementary motor area (pre-SMA) appears to be more  
20 directly related to temporal processing. SMA is divided into two different parts  
21 rostrocaudally (Picard & Strick, 2001): (i) the pre-SMA, whose phasic activation is  
22 related to spatial parameters of the forthcoming movement, and (ii) the SMA-  
23 proper, which exhibits phasic movement-related activity time-locked to  
24 movement onset (Matsuzaka et al., 1992; Tanji, 2001). During repetitions, the  
25 temporal structure of the forthcoming movement is shaped by pre-SMA, whereas  
26 its implementation depends on SMA-proper activity (Kotz & Schwartz, 2011).  
27 Jantzen et al. (2007) illustrated the functional difference between SMA-proper  
28 and pre-SMA by modulating the context of the motor task. When the pacing

1 stimulus is suspended following a sustained auditory-paced tapping task, contrary  
2 to pre-SMA, SMA proper is equally activated irrespective of the pattern of  
3 coordination, whether syncopated (on the beat) or synchronized (off the beat).  
4 Contrary to cortical areas exhibiting context-dependent activations, the SMA  
5 proper would have “a more ubiquitous role in motor timing” (Coull et al., 2011), a  
6 hypothesis supported by the activation of that structure during non-motor timing  
7 tasks such as duration comparison (Coull et al., 2008). In sum, among those areas  
8 related to the control of movement, in which initiation and termination phases  
9 structure neuronal activity, and which are also activated by rhythmic movement-  
10 based sensory afferences, the SMA appears to be crucially linked to AMS.

### 11 3.1.3 *Functional Connectivity Between Auditory and Motor Areas*

12 Investigating the structural connectivity of premotor areas provides clues on how  
13 their functional role is achieved during AMS: being at the interface between  
14 sensory inputs from the thalamus, sensory cortices, and the primary cortex  
15 exerting a direct control on simple movements, they are the perfect candidates  
16 for regulating the temporal relations between afference-driven actions. Action–  
17 auditory perception coupling has long been evidenced, for instance by Chen et al.  
18 (2006; 2008b) who investigated the engagement of different parts of the  
19 premotor system, by contrasting distinctive action–perception conditions, passive  
20 listening, listening with anticipation to tap (listen then tap) and tapping, with  
21 subtraction analyses conducted on fMRI data (figure 3 A & B). Functional  
22 connectivity between auditory and dorsal premotor cortices was found to be  
23 effective during rhythmic tapping, as opposed to passive listening or listening with  
24 anticipation to tap, and was a function of metric saliency when subjects tapped in  
25 synchrony to isochronous rhythms. The ventral premotor cortex activity did not  
26 appear to be sensitive to the temporal complexity of the stimulus. However, it  
27 appeared to be directly engaged in the processing of action-related sounds, its  
28 activity being significant only during listening with anticipation and during tapping



1 (Chen et al., 2008a). Chen et al. (2009) concluded that auditory and motor  
2 functions, as well as their coupling, can be tracked within the premotor cortex.  
3 The auditory cortex also contributes to auditory-motor transformations. Within  
4 the auditory regions, the processing of spectro-temporal auditory patterns,  
5 initiated in the ascending auditory pathways and the primary auditory cortex  
6 (Nelken et al., 1999; deCharms et al., 1998; Fritz et al., 2003), is continued in the  
7 planum temporale (Obleser et al., 2007; Nourski et al., 2009; Belin et al., 2000;  
8 Griffiths & Warren, 2002), which occupies the posterior part of the superior  
9 temporal plane. The connections of the planum temporale with the dorsal  
10 premotor cortex (Schmahmann et al., 2007), and their role in the disambiguation  
11 of complex sounds, as well as the effects of lesions (Liégeois-Chauvel et al., 1998),  
12 and the neuroanatomical characteristics of musicians and their associated  
13 rhythmical proficiency in AMS (Meyer et al., 2012), argue for the primary role of  
14 the planum temporale in auditory-motor coupling.

15

16 The segregation of auditory afferences in two processing streams was  
17 hypothesized decades ago (Rauschecker, 1997). The role of the ventral auditory  
18 pathway would be to support sound categorization, in opposition to the dorsal  
19 pathway, emanating from the planum temporale (temporo-parietal junction area  
20 and ventral premotor cortex, Romanski et al., 1999), whose activity appears to be  
21 tuned to spatial parameters of the sound (Tian et al., 2001). The faster neural  
22 latencies of the dorsal stream (Camalier et al., 2012) argue nonetheless for the  
23 hypothesis of its role in processing time (Rauschecker, 2018). The dorsal pathway  
24 would transform acoustic information into motor representations (Warren et al.,  
25 2005) by providing the motor system with time-tracked relevant information  
26 (Karabanov et al., 2009).

### 3.1.4 Short-Term Memory Engagement During Ensemble Performance

1  
2 Musical performance in an ensemble is representative of auditory-motor  
3 synchronization. Musicians have to deal with the inherent complexity of the  
4 musical stream which can make beat identification challenging. Matching the  
5 central spectro-temporal representations of the stimuli with the predicted or  
6 learned ones 'stored' in the working memory has been proposed as a mechanism  
7 to decipher musical rhythms. Keller (2008) formulated the hypothesis that, in an  
8 orchestra, individual ongoing musical performance could be guided by predictions  
9 about the co-performers' ongoing actions, and supporting behavioural data was  
10 provided (Pecenka & Keller, 2009). Participants who perform best when asked to  
11 imagine the continuation of a five-beat sequence, and to judge the temporal  
12 acuity of a consecutively presented probe beat, were also those who  
13 demonstrated good performance in sensorimotor synchronization. The execution  
14 performance of musical pieces is logically altered by working memory load (Maes  
15 et al., 2015). When tapping in synchrony with progressively more complex and less  
16 metrically structured auditory rhythms, greater activity in the PFC of musicians  
17 ascertained the contribution of working memory in the deconstruction of complex  
18 temporal structure (Chen et al., 2008b). A temporally accurate hierarchical  
19 planning of action (Koechlin & Jubault, 2006; Koechlin et al., 2003), and the  
20 involvement of working memory (Petrides, 2005), mediated by PFC, have been  
21 proposed as explanatory factors for the superior sensorimotor synchronization  
22 ability of musicians (Chen et al., 2009). The functional division mentioned in the  
23 previous section supports this contribution. The duality of the SMA connectivity -  
24 pre-SMA having extensive connections with prefrontal cortex (Wang et al., 2005;  
25 Luppino et al., 1993), and SMA-proper projecting directly to motor and premotor  
26 cortices (Johansen-Berg et al., 2004; Luppino et al., 1993) as well as spinal cord  
27 (Luppino et al., 1994; He et al., 1995) - indeed bears this functional organization.  
28 The engagement of short-term memory processes of the PFC is a function of the  
29 complexity of the rhythm sequence as revealed by the comparison of cerebral

1 activities while listening to isochronous sequences vs. metrical or non-metrical  
2 sequences (Bengtsson et al., 2009).

3

4 In summary, a clear coupling exists between the brain areas that organize  
5 movement sequences and those in charge of extracting relevant auditory  
6 structure during AMS, beat identification in our specific case. The functional  
7 connectivity between auditory and motor areas, specifically reinforced during  
8 beat processing, allows the construction of temporally tracked motor  
9 representations in pre-motor areas. Behavioural and electrophysiological data, as  
10 well as the analysis of connectivity, do indeed support the sequencing of multiple  
11 movements in the SMA. On the one hand, specific contributions of pre-SMA  
12 receive input from working-memory-related structures and define the temporal  
13 relations of events. On the other hand, SMA-proper, close to the descending  
14 pathways, is logically assigned with an implementation role (Kotz & Schwartze,  
15 2011). A structure dedicated to the spectral and temporal analysis of complex  
16 sounds - the planum temporale - projects onto both dorsal premotor and prefrontal  
17 regions. This suggests a tight coupling between auditory and motor areas, with  
18 input to and from working memory. The present section has also outlined the  
19 whole functional neural loop including basal ganglia and the thalamus. The  
20 functional role of premotor areas is achieved through the involvement of the  
21 cortical outputs to the basal ganglia and the thalamus, which connects both  
22 subareas of SMA (Johansen-Berg et al., 2004), and the output pathway from the  
23 basal ganglia back to the cortex. We are now therefore focussing our interest on  
24 subcortical structures of the brain. The known contribution of cortico-basal  
25 ganglia loops in the contextualization of sensory information for motor learning  
26 (Graybiel, 1995) makes their involvement coherent in auditory-motor  
27 synchronization.

## 1                    **3.2    Basal Ganglia Fine Tune Movement Timing**

### 2                    *3.2.1    AMS and Basal Ganglia Dysfunction*

3    The putative role of basal ganglia in action timing is first supported by  
4    pharmacology. The impairment of the execution speed of a tapping task by  
5    antagonists of dopamine (Rammseyer, 1997) indeed points towards the  
6    association between dysfunctions of the dopamine system and motor  
7    synchronization impairment. Our understanding of AMS mechanisms has largely  
8    benefitted from the investigation of the abilities of patients suffering from  
9    Parkinson's disease (PD), characterized by the degeneration of dopaminergic  
10    neurons in the substantia nigra pars compacta inducing a decrease in striatal  
11    dopamine content (Hornykiewicz & Kish, 1987; Kish et al., 1988). The pathology  
12    alters the balance between direct and indirect pathways which have opposite net  
13    effects (excitatory vs. inhibitory respectively) on thalamic target structures. The  
14    loss of the nigrostriatal pathway, which excites the direct pathway and inhibits the  
15    indirect pathway, consequently favours the latter at the expense of the former.

16

17    PD patients exhibit selective deficit in discriminating beat-based rhythms (Grahn  
18    & Brett, 2009). Compared to controls, patients at an early stage of the pathology,  
19    i.e. when dopamine depletion is restricted to the putamen and dorsal caudate  
20    nucleus, do not benefit from the presence of beats in the sequence to discriminate  
21    rhythms. PD patients completing auditory-paced repetitive flexion-extension of  
22    the wrist are known to exhibit less accurate inter-response intervals than controls  
23    for high frequencies (Pastor et al., 1992). Freeman et al. (1993b) reported larger  
24    variability of tapping rhythms among patients in addition to slower and higher  
25    rates than the reference below and above 3 Hz respectively. The fMRI data of  
26    patients during a finger tapping task (Elsinger et al., 2003) demonstrated a  
27    decreased activation within the sensorimotor cortex, cerebellum, and medial  
28    premotor system in PD patients compared to controls. Dopamine

1 supplementation restored brain activation patterns in patients but led to  
2 moderate if no performance improvement during task completion, evaluated in  
3 terms of accuracy and variability. The lack of performance increase with  
4 dopamine, also reported by O'Boyle et al. (1996), in conjunction with brain  
5 activation restoration, is intriguing. In an attempt to conciliate these findings,  
6 Cameron et al. (2016) asked PD patients and controls to complete a rhythm  
7 discrimination test. The performance of the PD patients, which was below that of  
8 the controls, was more affected by the complexity of stimulus metricality when  
9 they were off medication: in other words, medication increased their sensitivity  
10 to simple rhythmic changes and decreased their sensitivity to complex rhythm  
11 changes. Even if this appears as a confirmation of basal ganglia function, which is  
12 supposed to be partially restored by dopamine, in beat perception, clear  
13 explanations of medication-related performance alteration in the presence of  
14 complex stimuli are still needed. ((LOIC > CHECK THAT THIS CHANGE IS OK))

### 15           **3.3    Cerebellum Circuitry Predicts Sensory Input in AMS**

16 When reviewing behavioural data, we found a general agreement for the main  
17 contribution of the cerebellum to duration-based timing, evidenced by the  
18 alteration of the timing abilities of patients affected by cerebellar lesions (Ivry et  
19 al., 1988; Moberget et al., 2008; Grube et al., 2010a), or by the disruption of  
20 cerebellar function with rTMS (Grube et al., 2010b). However, recent research has  
21 extended the implication of the cerebellum to beat-based timing. For instance,  
22 Paquette et al. (2017) used voxel-based-morphometry, a neuroimaging technique  
23 which reveals the relation between behavioural variables and gray matter signals  
24 (Ridgway et al., 2008). They aimed to clarify the relation between inter-individual  
25 variations in gray matter volumes across the entire brain and beat interval  
26 discrimination skills evaluated with Harvard Beat Assessment Tests. The data  
27 supported the involvement of the cerebellum in the beat finding and interval test.  
28 Measures of performance in cerebellar patients during temporally non-adaptive

1 (isochronous pacing) and adaptive (tempo-changing pacing) AMS and a perceptual  
2 tempo judgement confirmed a global temporal processing dysfunction (Schwartz  
3 et al., 2016). The fact that noticed impairments translated into increased  
4 asynchronies and impaired error correction, Penhune et al. (1998) and Schwartz  
5 and Kotz (2013) reinforced the conception of the cerebellum as a structure  
6 dedicated to the reduction of time relevant sensory input, i.e. the encoding of the  
7 sensory flow into temporal discrete events.

8

9 The sensory coordination feature of the cerebellum (Gao et al., 1996) also enables  
10 the cerebellar networks to act in a feed-forward way, anticipating the sensory  
11 consequences of the planned action (Bower, 1997; Mauk et al., 2000; Courchesne  
12 & Allen, 1997; Ito, 2005; Ramnani, 2006; Pisotta & Molinari, 2014). The inherent  
13 delay of information processing and motor response would spoil AMS with  
14 unbearable temporal errors if mere reaction were the brain's dominant  
15 functioning mode. The existence of delays in the sensorimotor system, as well as  
16 its limited resources, are compensated by anticipation, a growingly recognized  
17 brain function (Bar, 2007; Friston, 2005)).

18

19 The cerebellar circuitry thus seems to contribute to inserting the timing of sensory  
20 inputs into the motor output (box 2, section 7.2). The discrimination of events  
21 according to their temporal saliency, associated with temporally specific learning,  
22 builds a temporal representation of events in the sub-second range, a key  
23 determinant of auditory driven actions. The description of the cerebellum as a  
24 brain structure in which online afferences and previous patterns of activations are  
25 compared and recognized, i.e. the very sensory coordination feature of the  
26 cerebellum (Gao et al., 1996), thus considers the whole cerebellar network as a  
27 feed-forward structure, anticipating the sensory consequences of the planned  
28 action (Bower, 1997; Mauk et al., 2000; Courchesne & Allen, 1997; Ito, 2005;  
29 Ramnani, 2006; Pisotta & Molinari, 2014). Electrophysiological data support this

1 role. In extra-cerebellar rat structures (superior colliculus and thalamus), for  
2 instance, Crispino and Bullock (1984) reported a modulation of the relative weight  
3 of auditory afferent inputs when the cerebellum was electrically stimulated.  
4 Tesche and Karhu (2000) measured evoked MEG responses to somatosensory  
5 stimulations in humans. In their study, the median nerve or the finger was  
6 stimulated at a steady interstimulus interval. Random omission of the stimulus did  
7 not alter the sustained evoked activity of the cerebellum. Moreover, the existence  
8 of a refractory period in the cerebellar response, caused by preceding stimulus,  
9 suggests the persistence, within neural networks, of the temporal pattern of  
10 somatosensory stimulations during a few seconds. Therefore, sensorimotor  
11 coordination appears to benefit from a short-term template of expected  
12 afferences, offering the possibility to overcome the delays inherent to feedback  
13 control (Wolpert et al., 1998a).

14

15 The PPC maintains cerebellar prediction until task completion (MacDonald & Paus,  
16 2003; Wolpert et al., 1998b). In AMS tasks, Pollok et al. (2008) identified the  
17 cerebellum and the PPC as a functional unit: measures of tap-related phase  
18 synchronization in conjunction with neuromagnetic activity evidenced functional  
19 connectivity within a cerebello-diencephalic-parietal network before tap onset  
20 when the stimulus was isochronous. When the stimulus onset was randomized,  
21 an increase of the parietal–cerebellar functional connectivity was found after tap  
22 onset, and was attributed by the authors to the mismatch detection. The analysis  
23 of functional connectivity among professional musicians further suggests a  
24 positive influence of the functional interaction within a PMC–thalamus–PPC loop  
25 on timing precision (Krause et al., 2010). Interestingly, the role of the cerebello-  
26 diencephalic-parietal loop in anticipatory motor control was also confirmed by  
27 transcranial direct current stimulation (tDCS: direct stimulation with low current  
28 via electrodes contacting the head; Anodal tDCS increases neuronal excitability  
29 and cathodal tDCS decreases it) applied over the PPC while participants were

1 synchronizing their finger taps with auditory cues (Krause et al., 2014). In this  
2 study, PPC tDCS was found to affect finger synchronization, with performances  
3 being degraded by anodal tDCS and improved by cathodal tDCS, a result that was  
4 replicated in a population of musicians (Pollok et al., 2017). Repetitive transcranial  
5 magnetic stimulation (in rTMS, the application of a magnetic field in a targeted  
6 region of the brain elicits repeated electric pulses) over PPC ascertained the same  
7 dependence of the auditory and visual synchronization modalities on PPC activity,  
8 and confirmed the anticipatory processes taking place in this brain area (Krause et  
9 al., 2012). The fact that PPC tDCS affected synchronization, but not continuation,  
10 is also in agreement with the view of an afference-efference matching process  
11 within the PPC.

12

### 13 **3.4 Thalamo-Cortical Network Sustains Rhythmical Movement-** 14 **Auditory Couplings**

15 We have so far emphasized the role of basal ganglia, thalamus, SMA and  
16 cerebellum as key structures of the functional loop implementing rhythmical  
17 automatized movements (Kotz & Schwartz, 2010; Kotz & Schwartz, 2011). It  
18 appears that sequential movement preparation depends on SMA activity  
19 (Mushiake et al., 1990; Shima & Tanji, 1998), particularly when the task requires  
20 the update of motor plans (Shima et al., 1996). Once cycles are engaged and  
21 competing motor programmes eliminated (Mink, 1996), basal ganglia discharges  
22 are related to the encoding of the learned afference-action relationship and sub-  
23 movement completion (Mushiake et al., 1990). The whole ganglia-thalamo-  
24 cortical network is thus engaged in the self-generation of action and the control  
25 of its timing (Jueptner & Weiller, 1998). Since their discovery, direct versus indirect  
26 pathway models of basal ganglia have been refined in light of anatomical  
27 variations and have revealed intrinsic and extrinsic connections (Jahanshahi et al.,  
28 2015). This is important in order to understand the contribution of the ganglio-



1 thalamo-cortical loop to AMS. Crucially, SMA controls the activation of STN  
2 (directly connected to the substantia nigra pars reticulata, the principal output  
3 nuclei of the basal ganglia) via the hyperdirect pathway. This ensures the  
4 connection between motor cortical areas and the globus pallidus (Monakow et al.,  
5 1978; Kitai & Deniau, 1981) with shorter latency than direct and indirect pathways  
6 going through the striatum and the internal globus pallidus (Nambu et al., 2002).  
7 This cortico–subthalamo–pallidal pathway would allow the cortical activity to  
8 favour the emergence of the structure of the upcoming movement (Nambu et al.,  
9 2002).

10

11 In rhythmic tasks, matching the movement phase to exogenous cues relies on the  
12 capacity of the cerebellar-thalamo-cortical loop to encode an event-based  
13 temporal structure (Kotz & Schwartz, 2011; Coull et al., 2011). Temporal relations  
14 of task-relevant events and the timing of anticipated future events are conveyed  
15 by the cerebellar projections on pre-SMA and SMA via the thalamus. The “sensory  
16 coordination” hypothesis, which postulates the control of temporal parameters of  
17 the cortical activity by the cerebellum, adds a complementary role to the  
18 cerebellum, that of implementing “computational subroutines capable of  
19 entraining the firing rates of different neural populations” (Molinari et al., 2007).  
20 Hence, the cerebellum seems to contribute to the coupling between auditory  
21 stimuli and neural activities, in agreement with the two fundamental functions of  
22 cerebellar processing identified by D’Angelo and De Zeeuw (2009): timing and  
23 sensorimotor adaptation.

24

25 The extraction of the temporal features of a predictable auditory sequence, the  
26 development of temporal predictions, and the coupling of action to salient  
27 auditory events thus require, in a complementary manner, the integrity of the  
28 ganglia-thalamo-cortical and cerebellar-thalamo-cortical networks (Dalla Bella et  
29 al., 2015). In addition, recent investigations of cerebellum connectivity with other

1 brain structures (Bostan et al., 2013) have evidenced an anatomo-functional  
2 interrelation between these two networks. Both subareas of the SMA are  
3 connected to the cerebellum: the non-motor domain of the dentate nucleus  
4 projects to the pre-SMA while its motor domain is related to the SMA proper  
5 (Akkal et al., 2007; Dum & Strick, 2003). There is a convergence of subcortical  
6 projections on the SMA from both the basal ganglia and the cerebellum, the  
7 former ones being more represented than the latter ones (Parthasarathy et al.,  
8 1992; Inase et al., 1999; Akkal et al., 2007). Interaction between these subcortical  
9 structures, which still remains to be clarified, would make short latency influence  
10 of the cerebellum on basal ganglia possible. Chen et al. (2014) have indeed shown  
11 in mice the existence of a disynaptic pathway, originating from the cerebellum,  
12 able to alter the activity of striatal neurons. A substantial disynaptic connection  
13 from the subthalamic nucleus to the cerebellar cortex was also found in monkeys  
14 (Bostan et al., 2010). In sum, the rapid, two-way communication between basal  
15 ganglia and cerebellum captures a functional unit. The highly interactive circuitry  
16 between the cerebellum, the basal ganglia, and the cortex (for a review see  
17 Caligiore et al., 2017) supports the transmission of cerebellar timing predictions  
18 to the thalamo-striato-cortical processing streams.

### 19           **3.5    Coupling sensory and motor structures during AMS by** 20                           **considering external and internal rhythms as oscillators**

21 In our effort to understand the neural bases of AMS, we have summarized four  
22 decades of neurophysiological data, and we have built a rough scheme of the  
23 underlying operating networks. The global network - reviewed above - of brain  
24 structures and their interconnections contributing to the synchronization of  
25 movement with auditory cues (see figure 2B for a visual summary) constitutes the  
26 neurophysiological foundations on which functional and reciprocal influences can  
27 be understood. The classical view of brain area specialization - if it satisfies a rough  
28 understanding of structure-function relationships - does not account for the

1 complete dynamics of sensory-motor coupling, in which sensory and motor  
2 boundaries tend to vanish. Localizationism can only partially unveil AMS  
3 mechanisms, not only because of the interleaving loops, but also because of the  
4 exact nature of the coupling between auditory afferences and efferences. The  
5 main focus of interest needs to be on the functional connections between the  
6 brain structures which are bound together during AMS. For example, the  
7 contribution of the sensory cortex to motor control has been evidenced by the  
8 evocation of motor responses following stimulations of the primary  
9 somatosensory cortex (Matyas et al., 2010). This has shown how prominent the  
10 appraisal of functional connections is for the understanding of externally driven  
11 movements.

12

13 A hint at auditory-motor linkages can also be found in premotor cortex activation  
14 based on individual tempo preferences. In participants who passively listened to  
15 tone sequences embedding weak or strong beats, TMS of the primary motor  
16 cortex revealed larger motor-evoked potentials (MEPs) in ankle-driving muscles,  
17 in the presence of metrically strong sequences (Cameron et al., 2012). After having  
18 expressed a preference for slow or fast tempo, participants exhibited larger BOLD  
19 activity in the premotor cortex when they were presented with the tempo they  
20 most highly rated (Kornysheva et al., 2010). Moreover, inhibitory repetitive TMS  
21 over premotor cortex altered tempo preference (Kornysheva et al., 2011).  
22 Michaelis et al. (2014) hypothesized that preferred tempo could depend on an  
23 endogenous oscillator, which would translate into spontaneous motor tempo and  
24 preferred perceptual tempo. The authors experimentally identified the latter as  
25 the natural tapping tempo of participants, and the former by asking participants  
26 to rate their preference for tone sequences in a series differing by their pace. Both  
27 were correlated. Moreover, when participants were listening to their preferred  
28 tempo, corticospinal excitability was modulated by the TMS of motor cortex  
29 during the tempo perception task (motor-evoked potentials being either

1 increased or decreased across individuals). These results show how rhythmical  
2 perceptual and motor tasks translate into action-perception synergies.  
3 Interestingly, protocols entailing measurements of behavioural and brain  
4 activations point towards the dependence of coupling magnitude on the matching  
5 between external and preferred rhythms.

6  
7 The coupling between dynamical systems through resonance has been proposed  
8 as a theoretical framework to account for this relation. Large and Kolen (1994)  
9 regarded the perception of rhythmical structures as a dynamical process: their  
10 model of entrainment — phase and frequency locking of oscillating networks with  
11 periodic events of auditory rhythms — emphasizes the temporal structuring of  
12 motor rhythms by incoming ones (Large, 2000). In the case of musical  
13 performance, internal self-sustained oscillations covering different periods would  
14 entrain to the rhythms of music (Large & Palmer, 2002). Before discussing the  
15 experimental evidence for and against this theoretical approach, we first describe  
16 the basic mechanisms of endogenous neural oscillatory activities.

17           3.5.1   *Oscillatory Neuronal Activity and Network Architecture Allow*  
18                           *Large Scale Neuronal Interactions*

19 The distinctive properties of the neuronal membrane ensure sharp variations of  
20 ionic conductance, which result in a depolarization followed by a  
21 hyperpolarization of the membrane potential. The waveform and features of this  
22 elementary membrane event, an action potential, are accurately predicted by the  
23 Hodgkin and Huxley model, which describes membrane conductance as a function  
24 of its potential. An action potential, often referred to as a spike due to its shape in  
25 electrophysiological recordings, occurs when a stimulus exceeds the  
26 depolarization threshold according to the all-or-none law. Synapses functionally  
27 fill the physical gap between neurons. In synapses, the electrical signal is  
28 converted into a chemical signal, in the form of a neurotransmitter release. The

1 subsequent binding of the transmitter to the postsynaptic receptors switches the  
2 signal back again into an electrical form. The type of coupling varies however  
3 according to the nature of the released transmitter, synapses being either  
4 excitatory or inhibitory.

5

6 However, it would be misleading to think of a neuron as a passive integrator, only  
7 ensuring the transfer of upstream information towards downstream connected  
8 cells in the form of action potentials. The neuron doctrine, already predominant  
9 before the 1980s, indeed put the emphasis on the connectivity of neurons  
10 modelled as bi-stable gates, with some computational ability (Llinás, 1988).

11 Membrane conductance to ions depends on the regulation of the opening of ion  
12 channel proteins. This regulation, referred to as gating, depends on the dynamical  
13 cooperation between several processes that we will not describe here in detail.

14 The diversity of channels included in the membrane, the regulation of their  
15 expression, and their opening kinetics all give rise to a complex integration ability  
16 at the neuron level, beyond its activation threshold and the associated bi-stability.

17 A clocklike neuronal activity lies in the range of patterns of a single cell, but it also  
18 includes transient and sustained firing, as well as subthreshold oscillations,  
19 depending on the physiological conditions such as the ionic concentration and the  
20 presence of neuromodulators. In other words, the neuronal excitability exhibits a  
21 large repertoire of possibilities (Connors & Regehr, 1996), among which  
22 oscillations, when the time occurrence of spikes is periodic (König, 1994; Kaneoke  
23 & Vitek, 1996). This is the first organizational level of brain oscillatory activity  
24 (figure 1B, Stiefel & Ermentrout, 2016).

25

26 Experimentally, the dynamical properties of neurons have been investigated by  
27 recording the firing of single cells in response to alterations of their potential. Puil  
28 et al. (1986) used frequency-domain techniques to model the contribution of  
29 passive and active neuronal membrane properties to input–output relationship.

1 They varied the frequency of the small amplitude perturbations of the membrane  
2 voltage, observed the neuronal voltage response and calculated the neuronal  
3 impedance, i.e. the frequency dependent resistance. The membrane (modelled as  
4 a capacitor), separate charges, and ion channels (modelled as a resistor) allow  
5 charged particles to flow (or to leak): the combination of a capacitor and a resistor,  
6 characterized by a time constant which represents the time necessary to reach a  
7 new steady state when voltage across the membrane is modified, passive  
8 properties of the membrane low pass filter voltage variations. Voltage-gated ion  
9 channels, modelled as an inductance, yield an active process ensuring the  
10 responsiveness for high-frequency variations of membrane potential. The  
11 combination of low- and high-pass filtering properties gives distinct frequency  
12 preference to neurons (Pike et al., 2000) and qualifies them as a resonant system  
13 (Hutcheon & Yarom, 2000).

14

15 Given that the hallmark of neurons is their connections, the collective functioning  
16 of cells should be considered. The examination of the local synaptic circuitry in the  
17 brain and in the spinal cord reveals one widespread pattern, the reciprocal  
18 connections between excitatory and inhibitory neural populations: action  
19 potentials originating from the former excite the latter, triggering the inhibition of  
20 the former (Hoppensteadt & Izhikevich, 1996). By measuring how the discharge of  
21 one neuron can be temporally shifted by perturbations such as post  
22 excitatory/inhibitory potentials, scientists have been able to draw its phase-  
23 response curve (PRC), which consists in plotting the normalized spike time shift  
24 against the perturbation time (Achuthan et al., 2011). Knowing the PRC of coupled  
25 neurons allows theoretical predictions about their phase difference (Stiefel &  
26 Ermentrout, 2016). Those predictions, in addition to the PRC, should consider the  
27 intrinsic firing rate of the neurons and the coupling strength. In the case of two  
28 identical coupled neurons, if PRC is characterized by a positive slope at zero  
29 crossing, the phase difference between neurons is progressively reduced to zero

1 (cf. figure 1B). This functional unit responsible for periodic activity is called a  
2 neural oscillator. Earlier, we mentioned the motor generation systems governing  
3 locomotion, which also depend on such functional organization (Marder &  
4 Calabrese, 1996). The phase convergence described between two coupled  
5 neurons can account for the fixed phase relation between CPG cycles (Marder et  
6 al., 2005). In the lamprey, the intersegmental time delay represents 1% of the  
7 cycle and is constant, irrespective of the swimming frequency (Cohen et al., 1992).  
8  
9 Oscillation is thus a key characteristic of neuronal activity, at the level of a single  
10 cell or for several neurons. The cellular organization of the cortex, which combines  
11 six layers of neurons of different types, is, however, much more complex, and  
12 loosens causal links between elementary neuronal processes and cortical  
13 oscillations. The observation of stochastic discharge in cortical cells (Softky &  
14 Koch, 1993; Stevens & Zador, 1998; Harsch & Robinson, 2000) appears to  
15 contradict the general shaping of brain activity by synchronous rhythms.  
16 Techniques such as EEG or EcoG, which aggregate signals from many cortical  
17 cells, nevertheless provide access to the measure of identifiable rhythms despite  
18 their limitations. EEG signals are recorded from the scalp and hence suffer from  
19 poor localization. Invasive measurements obtained by electrodes placed on the  
20 surface of the cortex are not spatially diverted by bone structure, dura and  
21 cerebrospinal fluid in EcoG. In animals, the insertion of deep microelectrodes in  
22 the brain can provide access to mesoscopic local field potential. Among the above-  
23 cited electrophysical techniques, rhythms recorded in LFP, spatially the most  
24 precise technique by summing signals with a radius of a few hundred  $\mu\text{m}$  (Xing et  
25 al., 2009), cannot be intuitively deduced from the stochastic spike trains of single

1 cells (Mureşan et al., 2008; Jarvis & Mitra, 2001). This discrepancy represents a  
2 challenge for “spike-to-spike synchrony”. The phase response characteristics of  
3 neurons modelled as periodic oscillators indeed entail synchronization with or  
4 without weak noise. In contrast, Brunel and Hakim (1999) modelled a population  
5 of inhibitory interneurons randomly connected by delayed synapses whose  
6 activity is dominated by a large background noise. Beyond a specific coupling  
7 strength, the amplification of perturbations in a network of strongly coupled  
8 neurons yields the emergence of high frequency collective oscillations. The “firing  
9 rate synchrony” framework (Brunel & Wang, 2003) proposes to explain network  
10 oscillations in terms of network architecture and intrinsic single neuron properties  
11 (Geisler et al., 2005; Moca et al., 2014). It can account for fast cortical oscillations  
12 which contrast with random and sparse spike trains of single cells (Fries et al.,  
13 2001b). Establishing the exact causal links between cell properties and the  
14 emergent dynamics of neuronal networks is a broad area of research, beyond the  
15 scope of the present review. The accumulation of knowledge on brain  
16 electrophysiological properties at multiple scales hints towards the conjunct role of  
17 the dynamical properties of elementary elements, and the diversity of neuronal  
18 connections (Wang, 2010). The development of techniques giving access to the  
19 simultaneous recording of multiple single cells (Buzsáki, 2004; Le Van Quyen &  
20 Bragin, 2007; Kobayashi et al., 2019; Jun et al., 2017; Mitz et al., 2017) will  
21 probably lead to a breakthrough in our understanding of the emergence of network  
22 dynamics (LOIC is this change ok?) from the properties of individual neurons.



1 Electrophysiological techniques nevertheless reveal oscillations in several bands  
2 (covering frequencies from 0.05 Hz to up to 500 Hz in the case of EcoG) during  
3 diverse behavioural states (Berger, 1929; Kahana et al., 1999). The frequency  
4 range measured in human EEG is generally divided into frequency bands: delta (0  
5 – 4 Hz), theta (4 – 7.5 Hz), alpha (8 – 13 Hz), beta (13 – 30 Hz), gamma (30 –  
6 100 Hz). These rhythms have been linked with behavioural correlates, despite the  
7 absence of a precise definition of their functional role. Alpha waves, recorded over  
8 sensorimotor cortex and prone to be phase-locked to stimuli (Sabate et al., 2011),  
9 are often associated with the facilitation of cortical information processing and  
10 working memory (Başar et al., 1997; Palva et al., 2005). ((LOIC you have forgotten  
11 to delete the following sentence))~~They decrease or desynchronize with movement~~  
12 ~~(Niedermeyer, 1997)~~. Beta- and delta-waves, both prevalent in the motor cortex,  
13 have been shown to reflect the sensibility to relevant sensory cues in a motor  
14 context (Saleh et al., 2010): they are prominent during the preparation of the  
15 movement, cease at its onset (Jasper & Penfield, 1949), and increase if the  
16 movement is withheld (Pfurtscheller, 1981). The stimulus-induced response in the  
17 beta band depending on anticipation (van Ede et al., 2014), beta oscillations also  
18 seem to contribute to a top-down modulation of sensory processing (Caras &  
19 Sanes, 2017). Gamma band would convey the sensory processing of auditory  
20 information (Gurtubay et al., 2004; Steinschneider et al., 2008) and would  
21 participate in the selection of salient stimulus. Fast gamma oscillations of the  
22 motor cortex also appear to engage in the active part of the voluntary motor  
23 action (Cheyne et al., 2008), even if their variability with respect to the ongoing  
24 movement challenges their association with specific aspects of the motor  
25 command (Donoghue et al., 1998). The gamma-band power is larger during the  
26 first repetition of a series of movements (Muthukumaraswamy, 2010).  
27 Consequently, gamma activity seems to be uncorrelated to movement sensory  
28 feedback. A more global role of gamma rhythms has been proposed, binding the  
29 activity of remote populations of neurons (Womelsdorf et al., 2007; Fries, 2009),

1 which could be involved in the formation and maintenance of motor plans  
2 (Donner et al., 2009; Pesaran et al., 2002). This hypothesis would explain the  
3 alteration of gamma-band power when participants face competing motor  
4 responses (Gaetz et al., 2013). Low frequency theta oscillations would contribute  
5 to the behavioural adjustments following the detection of an error. For example,  
6 theta oscillations elicited by sound in the fronto-temporo-parietal network are  
7 modulated in phase and power when detecting deviations in a sequence of  
8 standard tones (Hsiao et al., 2009; Recasens et al., 2018).

9

10 Today, experimental data converge towards a crucial role of cortical oscillations in  
11 the binding features of sensory modalities. However, their role in performing an  
12 audio-triggered movement is debatable (van Wijk et al., 2012). During auditory-  
13 cued tapping, a significant coherence was observed in the alpha band within the  
14 extensive brain network contributing to AMS, i.e. in the motor and premotor  
15 cortices, posterior parietal cortex, auditory cortex, thalamus, and cerebellum  
16 (Pollok et al., 2005). Being broadly distributed across cortices, oscillations would  
17 recruit functional networks in the service of behavioural control (Narayanan et al.,  
18 2013). The long-distance spreading of oscillations between brain structures raises  
19 the question of the nature of the relation between network fluctuations and  
20 ongoing behavioural dimensions. Looking more closely at how afferences  
21 influence brain waves may help to better understand the possible embedding of  
22 synchronization-related information within neuronal oscillations.  
23 Electrophysiological measures have indeed unravelled the relation between  
24 sensory processes and neuronal activity. The excitability of a neuronal population,  
25 which synchronizes at a given frequency (Buzsáki & Draguhn, 2004), depends on  
26 the phase of the oscillation. The perceptual framing of vision could be partly  
27 explained by the phase of the cortical alpha rhythm. The probability of perceiving  
28 two visual stimuli as being simultaneous is indeed minimal when the stimulus  
29 onset is locked to the positive peak of the alpha cycle. It is maximal when the

1 stimulus onset is locked to its negative peak (Varela et al., 1981; Gho & Varela,  
2 1988). Using the target auditory oddball paradigm, which consists in identifying  
3 task-relevant auditory tones intermixed with irrelevant ones, Haig and Gordon  
4 (1998) reported a dependency on the pre-stimulus alpha phase synchronicity of  
5 the participants' reaction time (figure 4A). An accumulation of evidence highlights  
6 the effect of ongoing central oscillations on sensory processing (Arieli et al., 1996;  
7 Fries et al., 2001a; Kiskey & Gerstein, 1999; Kruglikov & Schiff, 2003). The  
8 importance of this relation is reinforced by the nested modulation of the phase of  
9 each frequency band by the lower one in the auditory cortex (Lakatos et al., 2005).  
10 This hierarchy opens the possibility for a stimulus to structure the whole temporal  
11 activity of the cortex.

12

13 In summary, the present description of brain rhythmicity from single cells to  
14 interconnected networks legitimates the use of dynamical modelling. However,  
15 despite the functional importance of rhythmic activities within the brain, we need  
16 to clarify the influence of external rhythms on brain activity in the context of AMS.

### 17 3.5.2 Evidence of Cortical Entrainment by Auditory Rhythms

18 The experimental validation of the coupling between auditory and endogenous  
19 rhythms proposed by Large and Kolen (1994) currently remains challenging. If  
20 there is no doubt that neural networks can spontaneously oscillate (Hoppensteadt  
21 & Izhikevich, 1996; Llinás, 2014; Yuste et al., 2005), establishing their  
22 *entrainability* in the presence of auditory stimulations raises methodological  
23 difficulties. Neuronal entrainment, defined as the “alignment of ongoing neuronal  
24 activity to the temporal structure of external rhythmic input stream” (Lakatos et al.,  
25 2019), supposes (i) the restriction of frequency relationships among endogenous  
26 and external oscillators to harmonics (e.g. 2:1, 3:1), subharmonics (e.g. 1:2, 1:3),

1 or integer ratios (e.g. 3:2, 4:3; Large, 2008), and (ii) phase synchronization in the  
2 presence of stimulations matching the frequency range of neural oscillations.  
3 Auditory cortical activity satisfying (i) and (ii) in the presence of rhythmic patterns  
4 has proven to be common to different types of stimulation such as music, amplitude  
5 modulated noise or structured tones (Doelling & Poeppel, 2015; Henry & Obleser,  
6 2012; Arnal et al., 2015). An alternative explanation to the action of a neural  
7 oscillator is the so-called repetitive evoked response, according to which a rhythmic  
8 stimulus can give rise to a rhythmic input in the signal of the brain region processing  
9 it (Shah et al., 2004). We now briefly review the *pros and cons*, which have  
10 recently fed a lively debate on the possibility of directly assessing auditory  
11 entrainment in the brain.

12  
13 By recording the EEG activity of participants listening to musical samples  
14 including beats, Nozaradan et al. (2011) found a sustained periodic EEG response  
15 tuned to the frequency of the beat. The authors also evidenced the dependency  
16 of EEG response on metre interpretation. Specifically, when participants were  
17 asked to judge whether samples corresponded to a binary or a ternary metre,  
18 additional periodic signals at the corresponding subharmonics of the original  
19 tempo emerged in the frequency spectrum. The adjustment of neuronal  
20 activities within a limited frequency range, evidenced by steady state-evoked  
21 potentials observed in the EEG spectrum at frequencies matching the rhythmic  
22 pattern envelope (Nozaradan et al., 2012), opens the possibility to track the  
23 external rhythms back in the cortex. Similarly, in a neuromagnetic study (Fujioka  
24 et al., 2015), beta-band oscillations were found to depend on whether beats  
25 were perceived as accented or not, regardless of the origin of the accentuation,  
26 physically embedded in the stimulus or imagined. Tal et al. (2017) directly  
27 assessed the correspondence between the spectrum of neural activities while

1 listening and the modulation spectrum of the stimuli. Neural responses in the  
2 auditory cortex were enhanced at beat frequency, and, when the beat was  
3 omitted, remained phase-locked to the times of the missing beat. In a  
4 magnetoencephalography experiment using a pitch distortion detection task,  
5 Doelling and Poeppel (2015) showed that (i) the cortical oscillations were phase  
6 locked over a range of musical tempo, at least for tempo above one note per  
7 second in non-musicians, and (ii) entrainment was correlated with performance.  
8 In contrast, musicians' recordings showed entrainment across the whole range  
9 of the tested tempo. Neural plasticity, at the origin of the better performance of  
10 musicians compared to non-musicians, evidences the bidirectional nature of the  
11 relationship between behavioural and cortical entrainment. In short, the  
12 combination of high sensorimotor synchronization performance and high cortical  
13 entrainment among musicians supports the view that neural entrainment  
14 contributes to sensorimotor synchronization. A longitudinal study targeting the  
15 concomitant brain development and behavioural performances of musicians  
16 could clarify how neural entrainment and perception shape each other  
17 (Nozaradan et al., 2016a).

18

19 The results of these studies, in which the neural response mirrored the spectrum  
20 of the stimulus, were interpreted as evidences of cortical entrainment. This  
21 interpretation is in line with the neural resonance theory which assumes that beat  
22 perception involves the emergence of the internal periodic representation of a  
23 pulse through nonlinear coupling between neural oscillators (Large & Snyder,  
24 2009; Large et al., 2015). One specific resonance frequency range would translate  
25 into the observed selective neuronal activity adjustment. However, as per the  
26 definition of physical entrainment, we carefully stated in the first section of the  
27 present review that the occurrence of peaks of activity in the neural response at  
28 frequencies matching those embodied in the stimulus, while being consistent with  
29 neural entrainment, does not represent one self-sufficient evidence. Novembre

1 and Iannetti (2018) raised the possibility that steady state responses (SSRs),  
2 noticed in EEG responses when listening to auditory sequences (Nozaradan et al.,  
3 2011; Nozaradan et al., 2012; Doelling & Poeppel, 2015), might be driven by  
4 auditory event-related potentials (ERPs). Mancini et al. (2018) characterized the  
5 effect of prolonged and repeated stimulation on the main components of  
6 somatosensory ERPs and reported small amplitude ERPs despite habituation over  
7 repetition. One can argue that the amplitude of the ERPs measured by Nozaradan  
8 et al. (2011) may not have appeared to be measurable beyond the first stimulus  
9 of the sequence. But the contribution of ERPs, particularly the biphasic negative–  
10 positive (N–P) vertex wave and the contingent negative variation (CNV), cannot  
11 be fully discarded (Novembre & Iannetti, 2018). These ERPs are indeed both  
12 modulated by non-periodic attention and expectation (Nobre & van Ede, 2018).  
13 CNV in particular has been associated with auditory motor synchronization timing  
14 error correction (Jang et al., 2016).

15

16 The identification of prediction mechanisms is central for the understanding of  
17 neural processing which prevails during AMS. Breska and Deouell (2017) proposed  
18 to disentangle the predictions based on rhythm-dependent or rhythm-  
19 independent mechanisms by comparing temporal predictions based on rhythms  
20 to those based on memory. The ability of exogenous rhythms to entrain  
21 endogenous oscillations should depend on the periodicity of the stimulation: a  
22 periodic stream of beats is expected to be the most efficient input. Conversely, an  
23 alteration of the periodicity of the stimulation, obtained by jittering the inter-  
24 onset intervals, would be detrimental to the necessary period and phase  
25 adjustments of neural oscillations. Memory tracking of the time intervals, which  
26 can include knowledge of temporal contingency, would be less prone to be  
27 affected by the non-periodicity of the stimulation. In order to decipher the  
28 contribution of each type of temporal prediction, whether rhythm-based or  
29 memory-based, Breska and Deouell (2017) presented visual stimuli with either

1 periodic or jittered intervals to participants instructed to press a button on target  
2 appearance. The phase modulation of delta-band activity did not show  
3 dissimilarities between periodic and non-periodic conditions. This is the first  
4 outcome of this study: the limitation of EEG activity alignment as an indicator of  
5 entrainment despite the correlations with perceptual and behavioural  
6 performances (Snyder & Large, 2005; Stefanics et al., 2010; Besle et al., 2011;  
7 Henry & Obleser, 2012). A preparatory ERP analysis revealed similar waveforms  
8 across conditions, but differences were noticed when one expected stimulus was  
9 omitted. The long-negative component of the response, the CNV, known to be  
10 altered by the unexpected suppression of the imperative stimulus (Walter et al.,  
11 1964), was immediately resolved after the omission of one anticipated event for  
12 rhythm-based predictions, as if the stimulus was delivered. The vanishing of the  
13 negativity, despite the omission of the target, can be seen as the  
14 electrophysiological equivalent of the maintenance of cortical oscillatory activities  
15 after stimulus termination (Lakatos et al., 2013; Bartolo et al., 2014). When one  
16 self-sustained oscillator is coupled to a phase-resetting signal, upon the  
17 termination of this influential input, several oscillatory cycles are indeed expected.  
18 Breska and Deouell (2017) were, to our knowledge, among the first to report  
19 specific electrophysiological indicators of entrainment in the context of periodic  
20 rhythms. They were followed by Doelling et al. (2019) who attempted to  
21 specifically disentangle the two distinct mechanisms - neuronal entrainment and  
22 ERPs - in the presence of a structured auditory stream. They hypothesized that a  
23 neural oscillator would be a better prediction and would have more computation  
24 ability. They analysed the phase lag between neural response and acoustic input  
25 as a function of the stimulus rate. They predicted a larger phase lag as the stimulus  
26 rate increased for the evoked model, in contrast to a stable phase lag for the  
27 oscillator model. In agreement with the oscillator model, the MEG activity of the  
28 participants' auditory cortex revealed constrained phase regime while listening to  
29 music of varying note rates (1 to 8 Hz).

### 3.5.3 Auditory Entrainment Spreads Through Various Brain Structures

1                   3.5.3    *Auditory Entrainment Spreads Through Various Brain Structures*

2    The recent experimental evidence of auditory cortical entrainment in both

3    sensory and motor areas and at a specific tempo, as well as the hypothesis of an

4    encoding of the time of synchronization in neuronal oscillations, elegantly

5    legitimizes the use of dynamical models for the understanding of the interaction

6    of brain-auditory rhythms. However, neuronal oscillations do not only encode

7    information. They can also spread throughout connected populations (Buzsáki &

8    Draguhn, 2004), in such a way that the influence of behaviourally irrelevant stimuli

9    is lowered and the impact of relevant ones is reinforced. The technique of the

10   event-related potential (ERP), which consists in averaging the post-stimulus EEG

11   over a large number of trials, has been extensively used to disentangle the relation

12   between the underlying electrical activity of the brain and various cognitive

13   functions. Using this method in the context of AMS, significant differences

14   between accented and unaccented events related to metronome tones in

15   perceived and imagined metre have been reported (Schaefer et al., 2011) and

16   associated with top-down cerebral mechanisms of rhythm processing. This type

17   of control has also been evidenced with magnetoencephalography. Whilst

18   listening to identical click stimuli, Fujioka et al. (2010) contrasted the auditory

19   evoked responses from hippocampus, basal ganglia, and auditory and association

20   cortices related with "March" and "Waltz" metric conditions. In the former

21   condition, participants tapped every second click, while they tapped every third

22   click in the latter one. The neuromagnetic activity of several brain structures was

23   tracked during the listening period following the tapping task. In basal ganglia, the

24   larger response was found for March. Metric conditions elicited different

25   hippocampus activation latency: 80 ms for the march and 250 ms for the waltz.

26   The right temporal lobe activation also differed according to the metric contrast.

27   In the auditory cortex, the modulation of evoked response occurred at latencies

28   between 80 and 200 ms. Together, these results indicate that the hippocampal

29   memory system and the temporal processing system in the basal ganglia modulate



1 auditory cortical activity in this latency range, even in the absence of movement,  
2 but according to the specificities of the prescribed task. They reveal that neural  
3 activities induced by the metre context of musical samples facilitate the auditory  
4 perception of temporally relevant stimulus for the completion of a related motor  
5 task (Iversen et al., 2009; Grube & Griffiths, 2009; Pablos Martin et al., 2007;  
6 Snyder & Large, 2005; Brochard et al., 2003).

7

8 Gain modulation of event-related potentials and top-down control of rhythm  
9 perception thus represent convincing clues for the influence of external rhythm  
10 on the binding of sensory and motor areas of the brain. However, the shaping  
11 process of afferences by sensory pathways, e.g. brainstem response, during  
12 auditory synchronized movements, and the concomitant influence of corticofugal  
13 projections on this response have recently become a research focus. In order to  
14 clarify the encoding of sensory inputs, Nozaradan et al. (2016b) conducted an  
15 interesting study using the frequency tagging approach to simultaneously record  
16 brainstem and cortical EEG activity (figure 3 C, the frequency tagging method  
17 consists in using a stimulus with specific frequencies that can be easily isolated in  
18 the neural response). Participants, while listening to periodic amplitude-  
19 modulated tones, were instructed not to move or to tap in synchrony on every  
20 second beat. (LOIC do you mean here that the participant must neither move nor  
21 tap???) The frequency spectrum of the stimulus was set to elicit frequency-locked  
22 responses in the brainstem and in the cortex. The harmonic chord with partials at  
23 200, 400, and 600 Hz, and??? amplitude modulated at the frequency of 2.4 Hz,  
24 was likely to evoke a steady-state brainstem nuclei response at the frequency of  
25 the partial, and a steady-state cortical response modulated at 2.4 Hz. The authors  
26 compared two conditions: tapping at half the frequency of the amplitude  
27 modulation (1.2Hz) vs. passive listening. The increased cortical response at beat  
28 frequency during sensorimotor synchronization, compared to passive listening,  
29 was expected and measured, in accordance with the previous results of the same

1 group (Nozaradan et al., 2015). The maximal activity was measured at 2.4 Hz  
2 despite the movement frequency set at 1.2 Hz, which can be interpreted as a  
3 specificity of the AMS task. However, differentiating motor from auditory  
4 response remains subject to caution in this set of data. First, the existence of a  
5 peak of EMG activity at 2.4 Hz, in addition to the expected peak at 1.2 Hz, could  
6 explain EEG activity at 1.2 Hz and harmonics. The second potential source of motor  
7 overlap confound resides in the difficulty to separate sources in scalp-recorded  
8 EEG. The overlap of cortical motor and auditory activities in EEG can be addressed  
9 by alternative recording techniques. Ten Oever et al. (2017) used  
10 electrocorticography (EcoG) from one grid of electrodes implanted on the lateral  
11 frontal, temporal, and parietal lobes of one participant, ensuring a more robust  
12 mapping of the signal. Their protocol entailed detecting beeps embedded in white  
13 noise, with their intensity increasing monotonically over the trial presented at 1.5  
14 Hz. Participants were instructed to react the moment they perceived the sounds  
15 by pressing a button. The authors compared inter-trial coherence, which was  
16 expected to be high at the frequency of the stimulus presentation compared to a  
17 random sequence. Phase alignment indeed occurred before participants reported  
18 the stimulus as audible. On the contrary, auditory evoked responses were  
19 detectable after the beeps became audible. The same results were noticed in an  
20 experiment based on the same protocol with MEG recordings in 16 participants.  
21 As a solution for the limitation of low spatial resolution of EEG, the EEG-fMRI  
22 fusion method has been used by Li et al. (2019) to distinguish the neuronal  
23 populations that entrain to beat or metre. The spectra of auditory steady-state  
24 evoked potentials provided an indication of the entrainment ability of brain  
25 structures to beat (2.4 Hz) or metre (1.2 Hz). The thalamus, basal ganglia and SMA  
26 all exhibit peaks of activity both at beat and metre frequencies. The SMA was more  
27 prone to frequency locking at beat frequency than at metre frequency. Finally,  
28 with different measuring methods, Ten Oever et al. (2017) and Li et al. (2019)  
29 legitimize the conclusions of Nozaradan et al. (2016b).

1

2 The novelty of the Nozaradan et al. (2016b) study lies in the brainstem response.  
3 Auditory brainstem response is usually characterized by a transient response to a  
4 click, and a frequency-following response (FFR) to sustained periodic stimulations  
5 (Skoe & Kraus, 2010). The latter would reflect the basic processing of auditory  
6 information (Skoe & Kraus, 2010). Nozaradan et al. (2016b) reported a  
7 concomitant boosting of the brainstem responses, and the specific amplification  
8 of lower-pitched tone of the chord with no correlation with EMG tapping data.  
9 The observed gain modulation of the auditory response of the brainstem supports  
10 the view of an online modification of sound encoding during movement  
11 synchronization. The enhancement of the brainstem encoding during AMS could  
12 contribute to amplifying behaviourally relevant sound features. The efferent  
13 corticofugal projections (Musacchia et al., 2007; Chandrasekaran et al., 2009;  
14 Lehmann & Schönwiesner, 2014) could mediate the shaping of brainstem  
15 response by the cortex. Descending projections from the sensory cortex to the  
16 inferior colliculus appear to be crucial for the calibration of the auditory system as  
17 a function of experience (Bajo et al., 2010). Response properties of colliculus  
18 neurons are modified by the alteration of the cortico-collicular projection (Bajo &  
19 King, 2012). In bats, Ma and Suga (2001) set off shifts in the frequency-response  
20 curves of collicular and cortical neurons with electrical stimulation of the auditory  
21 cortex. The electrical stimulation of the somatosensory cortex extended the  
22 recovery period of auditory cortical neurons. Corticofugal projections can  
23 reorganize the auditory response of collicular and cortical neurons to specific  
24 features (frequency in the study cited above) of sounds (see also Yan & Zhang,  
25 2005). The contribution of non-auditory cortex shows that the reorganization  
26 could put the emphasis on behaviourally meaningful stimulus. Polley et al. (2006)  
27 demonstrated the possibility of eliciting a parameter specific plasticity in the  
28 auditory cortex by training rats to selectively attend to either the frequency or the  
29 intensity of auditory stimuli. The role of the corticofugal descending pathway in

1 driving experience-dependent plasticity, and more specifically musical processing  
2 ability, has also been evaluated in humans. In a MEG study, Coffey et al. (2016)  
3 revealed the cortical origin of FFR. They also reported a positive correlation  
4 between the strength of FFR and cumulative hours of musical training as well as  
5 between the strength of FFR and pitch discrimination thresholds. Over the past  
6 decade, researchers have gathered evidence of the joint contribution of cortical  
7 and subcortical components to FFR. The upcoming challenge lies in the  
8 disentanglement of their respective contribution to sound processing.

#### 9 *3.5.4 Oscillatory Activities of Interconnected Brain Structures Support*

##### 10 *Interdependence of Beat Tracking*

11 The perception of the auditory events to be temporally matched with movements  
12 appears as an intuitive prerequisite of AMS. We first opened this section with the  
13 neural substrates of beat tracking ability. We then introduced the experimental  
14 evidence of neural entrainment spreading. The detailed top-down supervision of  
15 the saliency of motor-relevant sensory information reveals the tight coupling  
16 between action and perception during AMS. Particularly, the fact that the  
17 voluntary organization of musical beats - in the form of metre imagery - can be  
18 tracked at the cortical level suggests its influence on perceptual ability. Selective  
19 enhancement of motor-salient frequencies by the cortex was supported by EEG  
20 recordings of cortical and subcortical activities (Nozaradan et al., 2018b): the  
21 former exhibited greater dissociation from the frequencies of the input than the  
22 latter by putting an emphasis on metre-related frequencies. The selective  
23 enhancement of metre-related frequencies does not fully rely on  
24 subcortical auditory properties, but is critically shaped at the cortical level,  
25 possibly through functional connections between the auditory cortex and other  
26 movement-related brain structures.

27

1 Action could therefore contribute to sharpening perception. Active sensing has  
2 been proposed in cognitive sciences and robotics, among other disciplines, to  
3 describe sensors which have not for sole input the energy from the sensed source:  
4 active sensing would also adequately describe most sensory processing  
5 (Schroeder et al., 2010). Being active involves perceptual exploration made  
6 possible, for example, by motor routines. Active sensing is a mechanism of the  
7 selective amplification of task-relevant auditory input. An example is the work by  
8 Morillon et al. (2014) who hypothesized that rhythmical movements would  
9 contribute to temporally sharpen the selection of auditory information.  
10 Participants tracking reference tones interleaved with distractors were found to  
11 perform better in target extraction when they were required to finger tap rather  
12 than during listening only (figure 4B). In the same vein, participants, when asked  
13 to listen to rhythms perceivable either as a binary metre or a ternary metre,  
14 exhibited neural activities larger at the frequency corresponding to the ternary  
15 metre if trained before listening (Chemin et al., 2014). These examples legitimate  
16 the vision of active sensing as a generalization of sensory-motor binding elicited  
17 by AMS. Sensory-motor experience thus appears to tune the temporal precision  
18 of predictions, and consequently shape perception with top-down processes.  
19 Descending processes have been evidenced in non-human primates with  
20 electrophysiological recordings. In non-human primates exposed to streams of  
21 pure tones and noise bursts interleaved with random acoustic patterns, Barczak  
22 et al. (2018) hypothesized that the detection of repeating patterns would require  
23 the entrainment of internal rhythms to demarcate the repeated rhythmical  
24 structures. They reported delta-phase locking, and the modulation of neuronal  
25 firings occurred earlier in the thalamus than in the primary auditory cortex. The  
26 recording of the sequence of endogenous rhythm alteration across central  
27 structures reveals the top-down processes during a task which necessitates the  
28 grouping of complex auditory patterns. This result also contradicts the definition  
29 of entrainment as an acoustically driven reflexive brain response (Novembre &

1 Iannetti, 2018). It indicates that the ability to identify rhythmic stimulus sequences  
2 without defined boundaries, solely characterized by their statistical regularities,  
3 *preludes* entrainment.

## 4 **4 Using Auditory Entrainment and AMS to Enhance** 5 **Locomotor Performance**

6 The previous section (3) presented evidence for the functional role of movement-  
7 based neural loops articulating ganglia-thalamo-cortical and cerebellar-thalamo-  
8 cortical networks, together with the dynamical properties of the locomotor  
9 system such as the vectors of synchronization of endogenous (i.e. biological) and  
10 exogenous (e.g. auditory) rhythms. Brain activations during AMS reveal that  
11 “motor-relevant” auditory cues functionally connect neural regions dealing with  
12 movement execution. This particular sensorimotor coupling legitimizes the use of  
13 auditory cues in order to influence the timing of motor actions and the success of  
14 its achievement. Appropriate spatio-temporal coordination of muscular  
15 activations is indeed necessary for movement production, and because temporal  
16 consistency often decides the success or failure of motor actions, it is a primary  
17 factor of performance. If the relation between locomotor performance and  
18 auditory stimulation is behaviourally substantiated, for example in the context of  
19 gait rehabilitation in PD patients, investigating the specific underpinning  
20 mechanism still only represents a partially explored research field. In this last  
21 section (4.1), we propose to investigate how the two types of entrainment,  
22 physical and neural, can be coupled to increase locomotor performance in walking  
23 patients and healthy runners.

### 24 **4.1 Biomechanical Entrainment as a Factor of Performance**

25 From the beginning of the nineties, bipedal robots - initiated by McGeer (1990),  
26 designer of passive dynamic walkers - have been built to walk downhill with

1 humanlike gaits, without actuation or perceptual control of any kind. Despite the  
2 absence of control of every joint angle, which makes complex computations  
3 unnecessary, passive walkers show a robust periodic limb trajectory, which  
4 restores itself if perturbed slightly. They are also categorized as limit-cycle  
5 walkers. The interaction between the inertial and gravitational mechanics of the  
6 two inverted pendulums which constitute the walker ensures a rather stable  
7 coordination (Collins et al., 2001). To enable ground-level walking, Collins et al.  
8 (2005) added small active power sources, in the form of ankle or hip actuation, as  
9 a substitute for gravity. In humans, the spring-like behaviour of the leg is not fully  
10 energetically conservative. While energy is stored in muscles and tendons during  
11 the impact absorption of the ground contact phase, and is reutilized during the  
12 supporting phase, some energy is also dissipated by muscle fibres when they  
13 lengthen. The maintenance of a limit-cycle behaviour is achieved at the energetic  
14 cost of muscular activation. The episodic supervisory control we introduced earlier  
15 thus appears as an efficient component when modelling locomotion control. The  
16 relative hierarchical organization of the CNS is combined with (i) the autonomy of  
17 peripheral networks in pattern generation, and (ii) the use of peripheral feedback  
18 to adapt movement kinematics. This fundamental feature of biological systems  
19 can find some resonance in this engineering model.

20

21 The observation of a limit cycle behaviour in the locomotor system, without  
22 supraspinal control (Gurfinkel et al., 1998; Gerasimenko et al., 2010), makes the  
23 passive dynamic model with reduced control a plausible model of CPG-driven  
24 walking (Miyakoshi et al., 1998; Aoi & Tsuchiya, 2007). Bipedal stepping stability  
25 of robots also benefits from peripheral sensors which can be used as state  
26 detectors, and provides input for the actuation (Miyakoshi et al., 1998). Similarly,  
27 in humans, beyond the evocation of fictive locomotion with peripheral  
28 stimulations, load afferences are required to sustain the emergence of a  
29 functional locomotor pattern (Dietz & Harkema, 2004; Van Wezel et al., 1997).

1 Finally, with behavioural measures showing gait entrainment towards a narrow  
2 range of periodic perturbations, the relative contribution of limit cycle oscillators  
3 in walking has been evidenced (Ahn & Hogan, 2012b). However, in a subsequent  
4 article, the same group proposed an alternative simple state-determined model,  
5 based on afferent feedback processes, independent of supraspinal control or  
6 oscillatory networks (Ahn & Hogan, 2012a). ((LOIC please check)) The associated  
7 phase locking of the perturbation within the locomotor cycle ensured the  
8 assistance of the propulsion phase. The primary benefit of limit cycle walking is  
9 indeed energy efficiency. Both artificial and biological systems are energetically  
10 optimal at their mechanical resonant frequency. Since oscillatory systems respond  
11 at greater amplitude when the frequency of their oscillations matches their  
12 resonant frequency, the cost of transport can be optimized by walking at the  
13 cadence at which periodic movement can be sustained with minimal contribution  
14 of actuators (Ahlborn & Blake, 2002).

15

16 For a given speed, the walking cadence lies in an interval ensuring less energy  
17 spending (Holt et al., 1991; Minetti et al., 1995; Umberger & Martin, 2007; Zarrugh  
18 et al., 1974; Bertram & Ruina, 2001). However, it is only recently that the ability  
19 of human adults to continuously optimize the energetic cost of walking has been  
20 demonstrated. Selinger et al. (2015) used robotic exoskeletons during normal  
21 walking to manipulate the metabolic cost landscape across the potential  
22 combination of stride length, stride frequency, speed, and associated energetic  
23 cost. The exoskeleton shifted the participants' optimal step frequency to higher  
24 or lower values than the one initially preferred by applying resistive torque.  
25 Participants were found to adapt their cadence to match the new optimal cadence  
26 despite the small amount of energetic gain associated with the updated cadence  
27 (< 5%). Energy efficiency thus does not appear only as an emergent property of  
28 the movement but can also be considered as an influencing input variable.

29



1 These findings provide the essential clues into understanding the benefits of  
2 auditory cueing during physical activities, for instance, when running in  
3 synchronization with music. If recommendations have to be formulated, the  
4 tempo should be chosen according to the properties of the limit cycle oscillator to  
5 maximize entrainment. This choice has at least two consequences. First, in the  
6 case of healthy walking or running, the normal and therefore most efficient  
7 cadence naturally represents the tempo value to match. We have indicated above  
8 that people are able to select their natural cadence, but obviously not in situations  
9 where other factors such as fatigue or pathology alter this ability. In the last  
10 section of the present review, we show how pathological gait (4.2) and running  
11 performance (4.3) can benefit from appropriate stimulations to counteract these  
12 side factors. The second consequence, somewhat linked to the first, is an “out of  
13 the lab” consideration. The practice of locomotor activities supposes different  
14 environments, durations, speeds and equipment according to the individuals or  
15 the training sessions: all these factors being prone to influence the natural  
16 cadence, the adaptability of the stimulation represents both a necessity and a  
17 technological challenge. The adaptability of the stimulation also leads us to  
18 consider its personalization as a promising way to address individual (non-  
19 )responsiveness.

#### 20 **4.2 Auditory Cueing During Walking of PD Patients Positively** 21 **Influences Cortical Networks**

22 The PD patients’ ability to initiate movement is impaired, due to reduced  
23 functionality of the ganglia-thalamo-cortical network accompanying the  
24 progressive loss of dopaminergic nigro-striatal neurons (Galvan & Wichmann,  
25 2008). This often gives rise to a freezing of gait, which is the transient difficulty in  
26 gait initiation or progression when approaching an obstacle or a turn (Giladi et al.,  
27 1992). The automatization of learned sequences is also altered (Wu & Hallett,  
28 2005). It was early hypothesized that the explanation for such deficits lie in the

1 impairment of internal cues generation to trigger the subsequent sub-movement  
2 in a sequence. During the execution of a visually cued sequence, preparation and  
3 execution movement times are known to co-vary with the reduction of the  
4 external cues in PD patients (Georgiou et al., 1994). Their difficulties in movement  
5 sequence completion, which can be reversed by external information, provide  
6 evidence of the role of basal ganglia in the release of relevant internal cues for the  
7 transition of movement stages.

8

9 Abnormal sustained activity in the beta band across the cortex and basal ganglia  
10 has been associated with the loss of dopamine neurons (Cassidy et al., 2002; Levy  
11 et al., 2002; Sharott et al., 2018; Kühn et al., 2005). Despite the mechanistic link  
12 between impairment in movement initiation and the alteration of the  
13 communication between brain structures (Engel & Fries, 2010), few studies have  
14 correlated objective measures of motor impairment and the amplitude of local  
15 field potential in the beta band (Brown, 2007). PD patients, who were implanted  
16 with neurostimulators in the STN, and who performed repetitive index finger to  
17 thumb taps, exhibited modulation of local field potential in the beta band  
18 (Androulidakis et al., 2008). As the movement became more bradikinetetic over trial  
19 time, the amplitude modulation of the STN activity decreased. Steiner et al. (2017)  
20 also recorded local field potentials simultaneously with motor performance  
21 several months after the implantation of deep brain stimulation electrodes. They  
22 assessed bradykinesia during a self-paced continuous alternating pronation and  
23 supination task which was completed as quickly as possible and with the largest  
24 amplitude possible. Oscillatory activity was suppressed in the beta band during  
25 repeated movements. The diminution of the beta band suppression was  
26 accompanied by the decline of the frequency and amplitude of movements.  
27 Fischer et al. (2018) recently assessed the role of beta activity in stepping by  
28 measuring the neural dynamics in the STN of PD patients implanted with DBS  
29 electrodes. They reported the suppression of oscillations in the beta band, time

1 locked to the gait cycle, following ipsilateral heel strike and contralateral foot  
2 raising. This modulation was increased when auditory cues assisted patients in  
3 timing their steps. A simultaneous reduction of step timing variability was noticed.  
4 Interestingly, in the presence of auditory cues, beta decreased before the  
5 ipsilateral heel strike became faster. The possible relation between the degree of  
6 step-related modulation of oscillations, influenced by auditory cueing, and  
7 movement performance in PD patients highlights the role of beta oscillations in  
8 the healthy brain. The beta reactivity of the STN, which is related to the saliency  
9 of cues with respect to future motor actions (Williams et al., 2003; Oswal et al.,  
10 2012), supports the role of basal ganglia in weighing the behavioural relevance of  
11 environmental information.

12

13 Providing an external clock would be prone to compensating for self-initiated and  
14 self-paced movement timing difficulties due to basal ganglia dysfunction. This  
15 would explain the missing internal cue at the origin of PD patients' difficulty to  
16 initiate and maintain cyclic movements such as walking (Rochester et al., 2010). If  
17 self-initiated and predictably cued movements indeed elicit the same levels of  
18 SMA activation in healthy participants (Jenkins et al., 2000), multiple arguments  
19 call for the dysfunction of the supplementary motor cortex in PD (Nachev et al.,  
20 2008) such as the decreased activity of pre-SMA and SMA observed in PD patients  
21 (Playford et al., 1992; Grafton, 2004). Caligiore et al. (2017) recently hypothesized  
22 a causal relation between alterations of the cerebellum to SMA circuit, the direct  
23 link between the SMA and the subthalamic nucleus (Nambu et al., 1996), and the  
24 impaired action sequencing of PD patients. The altered activity of SMA reported  
25 in PD patients would be associated with the decrease of the anticipatory activation  
26 of the STN by the hyper-direct pathway, a mechanism possibly prone to alter  
27 subsequent movement preparation in a sequence. Considering the overlapping of  
28 brain structures activated during movements relying either on internal or external  
29 cues, this model can be of interest in the context of AMS.

1

2 The deficiency of the basal ganglia–cortical circuitry necessitates some  
3 compensatory mechanisms that tend to maintain the temporal structure of  
4 actions to achieve coordinated movements such as those responsible for forward  
5 progression. Two explanatory hypotheses logically apply to patients' improved  
6 gait performance under the influence of auditory stimulation: (i) the residual  
7 activation of the basal ganglia by auditory cueing, and (ii) the compensatory  
8 mechanisms which originate from SMA (Eckert et al., 2006; Lewis et al., 2007)  
9 and/or from the cerebellum (Lewis et al., 2007). In the presence of an altered  
10 striato-thalamo-cortical loop which characterizes PD, compensatory timing  
11 mechanisms based on cerebello-thalamo-cortical circuits have been claimed  
12 (Dalla Bella et al., 2015; Lewis et al., 2007; Galvan & Wichmann, 2008; Kotz &  
13 Schwartze, 2011; Nombela et al., 2013). The overactivation of the cerebellum  
14 (Rascol et al., 1997) and motor cortex (Playford et al., 1992) measured with  
15 neuroimaging in PD patients during sensory-motor coordination is accompanied  
16 by functional changes, notably enhanced connectivity within the cerebello-  
17 thalamo-cortical loop (Palmer et al., 2010). Moreover, the dynamics of this  
18 connectivity appears to depend on the progress of the disease (Sen et al., 2010;  
19 Wu et al., 2011).

20

21 However, the balance between striato-thalamo-cortical and cerebello-thalamo-  
22 cortical circuits in PD remains an open research question. Miller et al. (2013)  
23 proposed to directly assess whether the striatal dopaminergic denervation,  
24 measured by reduced dopamine binding potential, would be associated with  
25 sensorimotor synchronization impairment. Patients finger tapped in synchrony  
26 with an isochronous tone sequence (500, 1000, 15000 ms inter-onset interval).  
27 Regression analyses conducted on the relation between synchronization accuracy,  
28 or variability, and denervation, did not appear very strong. Their conclusions, less  
29 straightforward than expected, finally call for a subgroup definition of patients: a

1 cluster analysis, yielding 3 subgroups of patients, substantiated the parallel  
2 degradation of synchronization accuracy, for the 500 ms target time interval, and  
3 the pattern of dopaminergic denervation. Patients with an asymmetric pattern of  
4 denervation between left and right hemispheres showed degraded timing ability  
5 for the corresponding affected hand, and patients with symmetric denervation  
6 showed similar degradation for both hands. This finding supports the contribution  
7 of striatal denervation to sensorimotor synchronization impairment. However, the  
8 subgroup of patients who had the largest proportion of striatal denervation  
9 exhibited the best synchronization performance compared to the other  
10 subgroups. The differences between subgroups suggest the existence of potential  
11 compensatory mechanisms: patients with advanced striatal denervation could  
12 have progressively switched to an alternative timing strategy over the course of  
13 the disease. Miller et al. (2013) related these results with the greater cerebellum  
14 activation. During a similar task, Jahanshahi et al. (2010) noticed finger tapping in  
15 synchrony with an isochronous tone at 1 Hz. Jahanshahi et al. (2010) found that  
16 cerebellar hyperactivation in patients was negatively correlated with the  
17 activation of the contralateral putamen during auditory-paced movements (Yu et  
18 al., 2007) and progresses with the disease (Sen et al., 2010).

19  
20 The existence of compensatory mechanisms raises the question of their evocation  
21 by AMS. In addition to the activation cerebellar networks, bypassing or facilitating  
22 the striato-thalamo-cortical loop has been proposed as explanatory mechanisms  
23 of gait improvement triggered by AMS. However, very few studies have attempted  
24 to identify the most prominent compensatory mechanism. Majsak et al. (1998)  
25 noticed bradykinesia when PD patients were performing maximal speed arm  
26 reaches toward a stationary ball, but not when they reached for a moving ball.  
27 This difference has been interpreted as a demonstration of the impairment of PD  
28 patients to move their limbs on a self-initiation basis compared to external  
29 stimulus-driven movements (see also Freeman et al., 1993a and Azulay et al.,

1 1999), in accordance with the hypothesis formulated by Goldberg (1985): the  
2 cerebellum, the parietal lobe, and the lateral premotor cortex represent the  
3 primary control loop for externally guided movements, whereas the basal ganglia  
4 and the supplementary motor area are more predominant in self-generated  
5 actions. Schenk et al. (2003) used a similar experimental paradigm encompassing  
6 reach-to-grasp movement in patients exposed to controlled deep brain  
7 stimulation (DBS). Patients implanted with a neurostimulator in the internal  
8 globus pallidum and the subthalamic nucleus show good improvement in tremor  
9 and bradykinesia (defined by Queen Square Brain Bank criteria as the “slowness  
10 of initiation of voluntary movement with progressive reduction in speed and  
11 amplitude of repetitive action” (Gibb & Lees, 1988)), and l-Dopa induced  
12 dyskinesias (Krack et al., 1998). In the same vein, Schenk et al. (2003) compared  
13 an externally timed condition (target moves away) and an internally timed  
14 condition (target is stationary) and found that auditory cueing used to initiate  
15 movement contrasted with the pursuit of a mobile target. This provided a cue for  
16 both movement initiation and execution. The second type of cue was more prone  
17 than the first type to influence movement execution parameters, such as the  
18 velocity profile. This conclusion calls for the use of more complex auditory  
19 stimulations than just a simple metronome. As expected, the effects of DBS on  
20 movement parameters were more pronounced in the internally timed condition  
21 than in the externally timed condition. The structures activated during visually  
22 guided movements include the superior parietal cortex, the premotor cortex, the  
23 thalamus, and cerebellar lobule VI. Conversely, activation of the basal ganglia, the  
24 supplementary motor area, the cingulate motor cortex, the inferior parietal, the  
25 frontal operculum, and the cerebellar lobule IV-V/dentate nucleus dominates  
26 when movements are internally generated (Debaere et al., 2003). Elaborating on  
27 these results, one can predict a more restricted influence of basal ganglia on  
28 auditory-cued movements than on self-initiated movements. This prediction was  
29 tested (Nowak et al., 2006) in PD patients with chronic stimulation of the

1 subthalamic nucleus, during a grip–lift task performed either at self-selected  
2 speed or in response to an auditory cueing signal. When DBS was off, auditory  
3 cues improved akinesia, restored grasp formation and compared to healthy  
4 controls. DBS was associated with excessive grip forces, irrespective of the type of  
5 movement initiation. In other words, auditory cueing contributed to movement  
6 initiation in patients, and DBS facilitated movement execution when lacking fine  
7 control. The premotor cortex, which is tightly connected with the cerebellum  
8 (Hoover & Strick, 1999), is responsible for the integration of environmental-  
9 related afferences, i.e. sensory mapping (Wise, 1985), and indirectly receives  
10 projections from the auditory cortices via the parietal areas (Pandya et al., 1969).  
11 Auditory motor coupling can consequently emerge from this alternative network  
12 (Weeks et al., 2001) as a substitute pathway to the damaged basal ganglia –  
13 supplementary motor area network. The restoration of fine motor control when  
14 AMS is applied to PD patients is also ascertained by muscular activation in the  
15 arms and legs. Their analysis revealed an increase in their symmetry and a  
16 decrease in their timing variability (Miller et al., 1996; Fernandez del Olmo &  
17 Cudeiro, 2003).

18

19 There is now convincing experimental evidence supporting the activation of  
20 compensatory pathways by AMS. However, the persistency of the contribution of  
21 impaired pathways cannot be wiped out, particularly under medication. The  
22 engagement of reward mechanisms in healthy participants completing physical  
23 exercise (see box 3, section 7.3) could also apply to PD patients, and help to  
24 maintain dopamine release. If phasic activity of SN DA neurons is considered as a  
25 reward prediction error signal (Schultz, 1998; Schultz, 2007; Schultz, 2016), Jin and  
26 Costa (2010) also showed its role in the signal initiation and termination of action  
27 sequences. The dual role of DA neuron supports the hypothesis of an effect of  
28 pleasurable auditory stimuli on PD motor deficits, mediated by the reward system.  
29 One consequence of dopamine depletion therapy, “compulsive singing” (Bonvin

1 et al., 2007), suggests the reciprocal influence of musical reward and dopamine  
2 release, which is the consequence of the involvement of basal ganglia in both  
3 rhythm and emotion processing (Troost et al., 2014). This behaviour is congruent  
4 with the beat-based timing impairment of patients, and its improvement under  
5 dopaminergic medication (Cameron et al., 2016).

6

7 The supervision of peripheral activities by higher levels of the CNS enables the  
8 contribution of alternative sensory inputs to the control of gait. This assumption  
9 opens the possibility of the manipulation of gait parameters by auditory cueing. In  
10 a seminal work, Thaut et al. (1996) demonstrated the benefits of auditory cueing  
11 on the improvement of parkinsonian patients' gait. Patients used auditory  
12 stimulations as a pacemaker during a 3-week training programme. Temporally  
13 predictable auditory cues had a post-training effect on gait by increasing gait  
14 velocity by 25%, stride length by 12%, and step cadence by 10% in comparison to  
15 self-paced patients who improved their velocity by only 7%. Benefits can  
16 generalize to non-cued gait after an extensive period of training with auditory cues  
17 (de Bruin et al., 2010; Frazzitta et al., 2009; Ford et al., 2010). However, Arias and  
18 Cudeiro (2008) argued that the grade of the patients' disability must be  
19 considered in order to observe gait facilitation. Other factors should also be  
20 considered because the success of this type of training varies significantly  
21 between individuals.

22

23 Beyond the patients' grade, Leow et al. (2014) showed that beat perception ability  
24 influences footstep synchronization with music. In recent studies, we proposed to  
25 identify the specific rhythmical abilities of patients, which may help to shed light  
26 on the functional mechanisms underlying the effects of AMS (Dalla Bella et al.,  
27 2017). The effect on gait parameters observed during auditory cueing in patients  
28 with PD was linked to their rhythmical abilities (figure 4C), especially their history  
29 of musical training and associated rhythmic skills (Cochen De Cock et al., 2018). In



1 another group of patients submitted to AMS for four weeks, where  
2 synchronization abilities were assessed before and after the training with auditory  
3 paced hand tapping and walking to auditory cues, individual responses to the  
4 training were either positive, neutral or negative, as measured by the distance  
5 covered during a six-minute walk test. A positive response to AMS was predicted  
6 by the synchronization performance in hand tapping and gait tasks. More severe  
7 gait impairment, low synchronization variability, and a prompt response to a  
8 stimulation change foster a positive response to AMS training. These findings  
9 experimentally demonstrate the role of general-purpose perceptual timing and  
10 sensorimotor abilities for gait rehabilitation in PD patients with auditory cueing.  
11 They can potentially be generalized as evidence of the functional link between  
12 such mechanisms and training strategies relying on neuronal plasticity. This link is  
13 supported by the recently unveiled link between cortical entrainment and  
14 synchronization accuracy. In the third section of the present review (3.5.1), we  
15 have indeed presented data showing the entrainment of EEG cortical responses.  
16 In the Nozaradan et al. (2016a) study, movement synchronization accuracy with a  
17 rhythmic beat could be explained by the amplitude of neural activity selectively  
18 locked with the beat period. Moreover, the strength of the endogenous neural  
19 entrainment was correlated with better temporal prediction abilities. These  
20 findings plead for the facilitation of AMS by neural entrainment.

### 21           **4.3    Running Performance in the Presence of External Auditory** 22                           **Pacing**

23 The use of synchronized music has also been proposed to runners, so that they hit  
24 the ground in time with the beats of a metronome or music. The example of the  
25 Ethiopian athlete, Haile Gebreselassie, who famously broke the indoor 2000 metre  
26 world record in February 1998 while the *Scatman* song was being played in the  
27 arena, is often cited to support the positive influence of auditory-motor  
28 synchronization on running performance (Simpson & Karageorghis, 2006; Bood et

1 al., 2013). As appealing as this interpretation may be, it should be considered with  
2 caution for at least two reasons. First, beat-step synchronization cannot be  
3 claimed in the absence of appropriate measures at high sampling rate. Second,  
4 the gap between Haile Gebreselassie's cadence (about 180 - 200 steps per minute)  
5 and the Scatman tempo (136 beats per minute) would only have made  
6 synchronization possible if he had adopted a syncopated rhythm (off the beat).  
7 Considering the ratio of the musical tempo to the runner's cadence - ideally 0.66  
8 in the case of syncopated rhythm - this type of synchronization would have  
9 remained stable if Haile Gebreselassie's cadence was close to 204 steps per  
10 minute. Higher cadence being associated with better performance, the music  
11 could have contributed to maintain the runner within the basin of highly efficient  
12 cadence. However, distinguishing the effects of auditory-motor-synchronization  
13 from those related to motivation is necessary because both coexist when  
14 motivational music is used. Haile Gebreselassie, who judged the "rhythm [of  
15 Scatman] perfect for running", could have benefited from motivational and/or  
16 attention diversion effects (see box 3, section 7.3).

17

18 The specific use of musical rhythm to maintain an optimal cadence nearing  
19 exhaustion has recently been clarified. Runners who synchronize their steps with  
20 the beat of a metronome see their time of exhaustion postponed during a high-  
21 intensity exercise compared to the same session conducted without stimulations  
22 (Bood et al., 2013). The associated decrease of the stride variability encouraged  
23 the authors to consider the consistency of the cadence as the explanatory factor  
24 of performance. There is indeed other evidence of the association between  
25 performance and stride rate variability, such as the decrease of the latter elicited  
26 by endurance training (Slawinski et al., 2001), or its increase with fatigue (Williams  
27 et al., 1991; Dutto & Smith, 2002). Similarly to Bood et al., Simpson and  
28 Karageorghis (2006) showed that synchronous oudeterous music (i.e. considered  
29 as neutral in terms of motivational qualities) can improve the performance of non-

1 elite runners in a 400 metre sprint. The musical beats could have acted as an ideal  
2 cadence maker, the stride frequency of recreational runners dropping  
3 dramatically well before the end of a sprint (Girard et al., 2016). In the experiment  
4 of Terry et al. (2012), the time to exhaustion of elite triathletes was also longer  
5 when they were listening to music considered as neutral in terms of motivation,  
6 compared to silence. Neutral music also decreased the perceived effort. The  
7 authors reported an improvement of running economy, which should be  
8 considered with care, the decrease of oxygen consumption [1.3-2.7%] remaining  
9 mostly within the range of measurement errors of the metabolic cart (2.5%,  
10 Medbø et al., 2012).

11

12 Morin et al. (2007) demonstrated the dependency of contact time and associated  
13 cadence on leg stiffness, as predicted by modelling the leg as a spring-mass  
14 system. The stiffness of the leg-surface combination is supposed to remain  
15 constant (Ferris et al., 1999; Ferris et al., 1998) in order to preserve the dynamics  
16 of the locomotor cycle (Farley & Gonzalez, 1996). However, Dutto and Smith  
17 (2002) observed changes in the stiffness characteristics of the leg during a run  
18 leading to fatigue. We can reasonably conceive that auditory beats delivered at  
19 the appropriate tempo could counteract the deleterious effects of fatigue on  
20 kinematics. This assumption could motivate further investigations. This approach  
21 would be an innovative strategy for the prevention of overuse injuries (Chumanov  
22 et al., 2012; Heiderscheit et al., 2011; Souza & Powers, 2009; Brindle et al., 2003;  
23 Fredericson et al., 2000; Geraci & Brown, 2005; Edwards et al., 2009; Wellenkotter  
24 et al., 2014; Williams et al., 2004; Williams et al., 2001; Granata et al., 2002). Stride  
25 variability is rarely characterized in the above-mentioned study despite its  
26 predictive value in the context of injuries. As revealed by detrended fluctuation  
27 analyses, step-to-step timing exhibits long-range correlations (Jordan et al., 2006),  
28 which, however, decrease over time during a prolonged run (Meardon et al.,  
29 2011). Interestingly, participants who suffered from previous injuries exhibited

1 lower long-range correlation than non-injured participants. The predictability of  
2 the stride interval decreasing with fatigue or injuries, together with the real-time  
3 measure of runners' stride time, could open interventional possibility through  
4 rhythmical auditory stimulation in an attempt to restore the kinematic complexity.

5

6 The contribution of auditory stimulation could be extended beyond the locomotor  
7 system, with the synchronization of two underlying biological rhythms, for  
8 instance locomotion and respiration. Locomotor-respiratory coupling (LRC) has  
9 been initially reported in quadruped animals as a mechanism transferring the  
10 mechanical deformations associated with locomotion onto the rib cage via the up  
11 and down movements of the visceral mass (Bramble & Carrier, 1983): the visceral  
12 piston mechanism results on locomotor dependent loading and unloading of the  
13 diaphragm, and alters the pulmonary volume. Animal studies revealed that the  
14 coupling is also neurological. Connections between locomotor and respiratory  
15 centres were evidenced by the increase of respiratory rhythm evoked by fictive  
16 locomotion (Waldrop et al., 1986) and the stimulation of peripheral muscular  
17 mechanoreceptors (Iscoe & Polosa, 1976). In quadruped mammals, the ratio of  
18 locomotor and respiratory frequencies is 1:1 (number of strides:number of  
19 respiratory cycles). However, bipedalism has significantly reduced the mechanical  
20 linking between both systems, the movement of the spine being nearly non-  
21 existent. The direct consequences are the multiplicity of possible ratios of  
22 frequencies (usually 3:2, 2:1, 5:2, 3:1) and potential independence of the phases  
23 of both systems (e.g. Bardy et al., 2015; Hoffmann & Bardy, 2015). The inspiratory  
24 and expiratory volumes ascribed to the visceral piston in quadrupeds reaches 20%  
25 of the tidal volume (Lee & Banzett, 1997), whereas in humans, estimates vary  
26 between 2% (Banzett et al., 1992) and 10-13% (Daley et al., 2013). How critical  
27 LRC is for energy efficiency is a matter of debate for additional reasons. First,  
28 evaluating the coupling of two systems, whose eigenfrequencies are different,  
29 remains challenging. Methods are debatable (Zelic et al., 2017) and the variables

1 which are used to appraise coupling are not obviously the ones most  
2 representative of the coupling. Most authors used the impact of the foot as the  
3 locomotor event of reference (McDermott et al., 2003), but the loading of the  
4 visceral mass, affecting lung volume, is initiated with a large delay with respect to  
5 foot landing. Second, the real contribution of LRC to pulmonary air exchange is  
6 debatable. In a recent study about LRC, Daley et al. (2013) postulated that the  
7 synchronization of the peak acceleration of the centre of mass, with the  
8 inspiratory and expiratory transitions, would be the preferred pattern used by  
9 runners to contribute significantly to the breathing mechanics. Further studies  
10 should challenge this specific hypothesis in order to provide a better  
11 understanding of the nature of the LRC in bipedal locomotion. More generally,  
12 how music as an exogenous AMS flows into multiple and mechanically coupled  
13 biological systems exhibiting various natural frequency ratios, such as the  
14 locomotor system and the respiratory systems, remains wide open for further  
15 investigation.

## 16 **5 Open Research Questions and Conclusions**

17 Explaining how physics and neuroscience contribute to the emergence of stable  
18 yet adaptable movements is one aim of behavioural science. The present review  
19 is an attempt to exploit this complementarity between the two approaches  
20 towards our understanding of AMS. Our first step consisted in identifying a  
21 relevant theoretical framework. If empirical studies are valuable to identify  
22 structures and networks in the brain involved in perception and action, modelling  
23 neural activity with dynamical systems provides a universal mechanism for the  
24 transformation of auditory information into efficient motor commands through  
25 oscillator-based coupling and entrainment principles. We demonstrated the  
26 appropriation of time-related information in the brain, and the relative  
27 segregation in different structures of the afferences according to their rhythmical  
28 characteristics and their salience in an action perspective. The notion of motor

1 salience of a given rhythm is empirically illustrated by the dependence of rhythm  
2 perception on anthropometric parameters of the listener (Todd et al., 2007). The  
3 dynamical properties of the locomotor system, which partly relies on oscillatory  
4 spinal networks, putting into motion a chain of articulated segments characterized  
5 by their eigenfrequencies, have only recently been clarified. Dynamical  
6 entrainment appears to be possible at both central and biomechanical levels,  
7 validating the limit cycle oscillator model as a relevant model of cyclical locomotor  
8 activities. In the presence of rhythmical auditory stimulations, the reciprocal  
9 influence of neuronal and behavioural entrainment substantiates the relevance of  
10 the dynamical system approach as an explanatory framework for SMS.

11

12 In this review, we have presented the multi-level distribution of auditory  
13 entrainment, from neural to biomechanical structures, or in other words, how  
14 auditory stimulations find their way towards the rhythmic locomotor system. The  
15 cited studies show the complexity of the functional attributes of the auditory  
16 stimulations. There is no doubt that we have learned an immense amount about  
17 neural responses over the past two decades. However, it is evident that much  
18 remains to be established about the precise mechanisms sustaining locomotor  
19 performances. Viewing sensory and motor functions in isolation probably does  
20 not help to discover the whole potential of auditory stimulations on motor  
21 performance, considering their tight coupling. Uncovering the whole chain of  
22 coupling factors between perception and action presents a surmountable  
23 challenge, and, inspired by the state of the art synthesized above, some  
24 recommendations for future research can now be made.

25

26 As legitimate as the analysis of living systems is, through the prism of dynamical  
27 systems, this theoretical framework does not explain all emergent properties of  
28 biological oscillators. The characteristics of movement kinematics during a  
29 synchronization task in particular are not fully explained. Some kinematic data

1 challenge the theoretical frameworks used to model synchronization. For  
2 instance, during a finger-tapping task paced by auditory beats, Balasubramaniam  
3 et al. (2004) noticed that the trajectory was roughly sinusoidal, but movements to  
4 and from the beat could be distinguished, breaking some predictions of the  
5 dynamical system theory. Specifically, the symmetry in position and velocity were  
6 not perfect, and movements towards the temporal target were found to be more  
7 rapid than movements ensuring the return phase. To demonstrate the link  
8 between timing and asymmetry, Balasubramaniam et al. correlated timing  
9 accuracy with movement kinematics, and indeed found a positive relation: the  
10 relative asynchrony, i.e. the early or late tap with respect to the auditory cue was  
11 negatively correlated with the subsequent return phase. The duration of the  
12 movement towards the cue was, on the contrary, relatively constant. The strong  
13 negative correlation between each phase bolsters the existence of a closed-loop  
14 error-correction principle, visible in the trajectory asymmetry. This set of data is  
15 not in complete agreement with open-loop or pure limit-cycle oscillator models  
16 accounting for repetitive movements, since these models do not account for  
17 movement asymmetry. A unifying model, reconciling consecutive event  
18 correlation and movement asymmetry, is still to be proposed.

19

20 If evidence of cortical entrainment by musical tempo has been now established,  
21 only a systematic investigation of the relation between sound inputs and neural  
22 outputs will reveal the neural mechanisms of sound perception. The shaping of  
23 cortical activity by sensory inputs indeed raises the question of the preceding  
24 processing stages which ensure the selective entrainment to metre-related  
25 frequencies (Nozaradan et al., 2018b). The embodiment mechanisms of auditory  
26 rhythms will be better understood after how rhythm complexity affects temporal  
27 selection has been clarified. In other words, the investigation of input–output  
28 nonlinear transformation of auditory rhythms and their contribution to the  
29 emergence of perceived beats should be continued. In this regard, if the mapping

1 of stimulus inputs and EEG outputs provides a macro description of the relation  
2 between stimulus properties and brain activity, it fails to reveal specific neural  
3 processes (Nozaradan et al., 2018a). ECoG recordings, which offer better signal-  
4 to-noise ratio than scalp-recorded EEG, could contribute to clarify the link  
5 between single stimulus presentations and cortical activity (Sturm et al., 2014).

6

7 Auditory rhythm perception can shape movement, but the opposite is also true. If  
8 moving one finger, or oscillating our body in time to music helps to feel the beat,  
9 can we consider this common practice as an evidence of dynamic attending?  
10 Chemin et al. (2014) showed that in participants listening to a rhythmical  
11 sequence before and after moving their body to this rhythm, the  
12 electroencephalographic responses to the rhythm were superior at the specific  
13 rhythm frequencies after body movement. Phillips-Silver and Trainor (2008), by  
14 demonstrating how influential passive motion of the head can be on rhythmic  
15 metric encoding, posited the vestibular input as a determining factor of rhythm  
16 perception, and outlined the cross-modal nature of the coupling between rhythm  
17 perception and movement. Vestibular and proprioceptive systems, as  
18 complementary sources of movement-related inputs, connect body movement  
19 and auditory rhythm processing (Phillips-Silver & Trainor, 2007; Phillips-Silver &  
20 Trainor, 2005). If disentangling the specific mechanisms of a reciprocal influence  
21 remains intrinsically challenging, the influence of movement on the perception of  
22 rhythmical cues has not only motivated the search for experimental evidence, but  
23 has also nourished a renewed theoretical approach of sensory-motor coupling. In  
24 a protocol entailing the disentanglement of two streams of sound on the basis of  
25 endogenous temporal cues, Morillon and Baillet (2017) evidenced the  
26 dependence of predictive timing on the activity of the motor system. They noticed  
27 beta neural oscillations directed towards auditory regions and the sharpening of  
28 the quality of temporal predictions, as well as better temporal selection of  
29 relevant auditory information with overt rhythmic movements. These results



1 reinforce the active sensing hypothesis which represents a relevant framework to  
2 investigate the interdependence between action and perception.

3

4 Top-down influences on rhythm perception should not be neglected either. In  
5 musicians presented with either a sequence of tones or blinking visual cues at the  
6 same frequency on which they were instructed to project a ternary metre, the  
7 electrophysiological responses exhibited an enhancement of the amplitude at the  
8 ternary subharmonic (one third of the stimulus frequency) across sensory  
9 modalities (Celma-Miralles et al., 2016). Recent studies precisely attempted to fill  
10 the gap between central and behavioural evidence of entrainment, by establishing  
11 a link between rhythmical perception and synchronization abilities with  
12 rhythmical auditory stimulations (Drake et al., 2000a), or their influence on gait  
13 rehabilitation (Nombela et al., 2013; Dalla Bella et al., 2015; Dalla Bella et al., 2017;  
14 Sihvonen et al., 2017). Cochen De Cock et al. (2018) reported a positive response  
15 to cueing, measured as an increase of walking speed, in 17 out of 39 non-  
16 demented patients with PD. These patients aligned their steps more often to the  
17 rhythmic cues, and showed better music perception than the 22 patients with  
18 non-positive response. In six of the patients, gait performance was worsened with  
19 rhythmic cues. Rhythmic and musical skills, which can be modulated by musical  
20 training, may increase beneficial effects of rhythmic auditory cueing in Parkinson's  
21 disease. These results point out how the personalization of auditory samples, as a  
22 function of rhythmical perception ability, will ensure the best therapeutic value  
23 for PD patients. The definition of the characteristics of rhythmical auditory  
24 stimulations, such as frequency matching and variability, is another venue of  
25 research to maximize the therapeutic effects of cueing. The temporal properties  
26 of variability are particularly important in gait which involves movement  
27 repetition. The temporal structure of cueing appears to influence the temporal  
28 dynamics of gait. Dotov et al. (2017) demonstrated that cueing with isochronous  
29 or randomly varying inter-stimulus/beat intervals removed the LRC in the stride

1 cycle. In contrast, persistent correlation in gait was unaffected with stimuli which  
2 mimicked the properties of variability found in healthy gait. The long-term  
3 consequences of biological variability embedded in stimuli should be investigated.  
4 Addressing this research question would also tackle the associated dilemma  
5 concerning the most beneficial type of cueing, synchronizing while sacrificing  
6 natural variability, or sparing natural variability but diminishing the positive effects  
7 of synchronizing with the cue. Interestingly, an extensive analysis of the spectrum  
8 of western music revealed that rhythm fluctuations follow the fractal relation  
9 (Levitin et al., 2012) and appear to contribute to the pleasure experienced by  
10 listeners (Hennig et al., 2011).

11

12 Despite the common belief associating rhythmical auditory stimulations, and  
13 particularly music which boosts sports performance, further research is required  
14 to clarify the physiological mechanisms likely to support this relation. The main  
15 challenge lies in the interconnection between physiological and  
16 neurophysiological factors, since music reinforces the connection between  
17 perception and movement, and probably alters the activity of motor networks and  
18 their associated physiological processes. In contrast with the developing  
19 literature, which aims to clarify the link between the rhythmic skills and  
20 therapeutic potential of auditory gait training, similar systematic investigations of  
21 the runners' gait, under the influence of music as a function of their perceptual  
22 ability, are still missing. A prerequisite could be the search for direct evidence of  
23 central entrainment during sports activities. Similarly assessing the entrainment  
24 potential of the locomotor system during running would complement the  
25 knowledge acquired on walking (Ahn & Hogan, 2012b). Beyond the use of periodic  
26 mechanical perturbations which entails the use of apparatus prone to alter the  
27 execution of fast movements, we believe that an innovative set up allowing the  
28 manipulation of the dynamical properties of the environment could bring some  
29 answers. In the presence of a time-dependent variation of ground stiffness (which

1 is a key determinant of the cost of transport and consequently governs running  
2 kinematics), how would runners explore this new dynamical environment? Would  
3 they adapt more quickly to the dynamics of the new environment in the presence  
4 of auditory cues? Such investigation of the balance between central and  
5 biomechanical factors would challenge our initial proposition of the existence of  
6 multi-level entrainment.

7

8 In conclusion, refining our understanding of how body movements are shaped by  
9 rhythm perception amounts to a better understanding of how action and  
10 perception are coupled. This dialogue is beautifully illustrated by the dependence  
11 of rhythm perception on body movement. Brain responses to rhythm are  
12 enhanced by previous movement performance (Chemin et al., 2014). The  
13 influence of anthropometric factors on preferred tempo (Todd et al., 2007) can  
14 also be seen as an embodiment of our movement repertoire within perception.  
15 The mechanism by which the brain favours task-relevant inputs (Lakatos et al.,  
16 2008) logically opens the possibility to manipulate movement performance with  
17 relevant sensory inputs. Action-based relevance of the stimulation appears as the  
18 primary factor to consider when the goal is to foster auditory-locomotor coupling.

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## 1            7    **Appendixes**

### 2            7.1    **Box 1: Information processing theory provides an alternative** 3                    **theoretical framework to capture auditory-movement** 4                    **synchronization**

5    The present review mainly focuses on biological and physical phenomena for  
6    which dynamical models are suitable. Information processing theory, which  
7    provides an alternative theoretical framework, is also relevant to analyse  
8    variability and error correction related to AMS tasks. Timekeepers represent the  
9    core of that theory, which supposes an explicit generation of discrete time  
10   intervals. Through this approach, the emphasis is consequently put on cycle-to-  
11   cycle measure and correction of motor timing. Error correction is crucial to sustain  
12   SMS because of the inherent variability of movements (Woodworth, 1899; Fitts,  
13   1954). When plotted in the phase plane, the kinematics of biological movements,  
14   for instance finger flexion/extension during tapping, or bimanual coordination,  
15   appears as the superposition of partially recovering closed curves which describe  
16   a band (figure 5A).

17

18            Linear timekeeper models have been particularly relevant to explain data  
19   obtained in the continuation tapping paradigm, in which participants are  
20   instructed to tap in synchrony with a metronome and continue to tap at the same  
21   tempo after the auditory pulses have been turned off. This paradigm reveals the  
22   ability of human participants to maintain a mean tapping rate close to the  
23   reference value while the variability increases with the duration of the interval  
24   (Stevens, 1886). Moreover, inter-tap interval duration during the continuation  
25   phase is negatively correlated with the interval duration at lag one, i.e. there is an  
26   alternation of longer and shorter intervals compared to the original prescribed  
27   period. Wing and Kristofferson (1973b) proposed a model (W-K model, figure 5 B)

1 to account for the mean and the variance of the inter-response intervals. In the  
2 W-K model, a central timer generates intervals subject to temporally variable  
3 motor implementation due to motor delays. Both the clock and the motor delays  
4 possess their own variance, which can be estimated (Wing & Kristofferson, 1973a).  
5 Vorberg and Wing (1996) established the increase of clock variability with  
6 decreasing movement frequency, whereas the variability related to motor delay  
7 was found to be constant (Wing & Kristofferson, 1973b; Vorberg & Wing, 1996).  
8 Hence this combination associates an increase of the total variance, i.e. the  
9 variance of the intervals' durations, with lower movement frequency. The  
10 increase of perceptual variability with interval duration, predicted by the model,  
11 has been measured experimentally (Friberg & Sundberg, 1995).

12

13 In addition to drift, the existence of long-period fluctuations has also been  
14 reported, as early as 1886 by Stevens (1886), who noticed "larger and more  
15 primary waves" as opposed to "constant zig-zag". Many biological rhythms follow  
16 a mathematical law ( $1/f$ ) (Gilden, 2001; Van Orden et al., 2003). In the case of  
17 rhythmical motor activities, it is expressed as long-range correlations or long  
18 memory of the duration of intervals, which tend to be correlated with the duration  
19 of intervals that occur immediately after, as well as with the duration of intervals  
20 that follow much later in the series (Torre et al., 2011; Yamada, 1995; Roberts et  
21 al., 2000). Fluctuations in tempo, even if they are more marked during tapping  
22 synchronization continuation, are still present during sensorimotor  
23 synchronization (Chen et al., 1997). Power spectra of interval fluctuations of  
24 participants who are instructed to reproduce temporal intervals, exhibit linear  
25 negative slopes at low frequencies and linear positive slopes at high frequencies,  
26 representative of  $1/f$  and white noises respectively (Gilden et al., 1995). The  
27 mixture of noises embedded in the data, as well as numerical simulations,  
28 encouraged the authors to consider the central time keeper of the W-K model as  
29 a source of  $1/f$  noise and the motor command as a source of white noise. With

1 some adaptation of its parameters, the W-K model is still considered as a solid  
2 paradigm by the advocates of the existence of a central time keeper.

3

4

5 **7.1 Box 2. The cerebellar architecture ensures the mapping of**  
6 **sensory information into temporally relevant motor**  
7 **commands.**

8 Imagery studies associate the cerebellum with AMS (Pollok et al., 2005).  
9 Moreover, the transient alteration of cerebellar function with TMS entails an  
10 impairment of synchronization performance during paced finger tapping,  
11 evidenced by an increase of the variability of the intertap interval (Del Olmo et al.,  
12 2007). These experimental clues should not hide the debate about the cerebellar  
13 contribution to beat based timing.

14

15 Since cerebellum has been under the scrutiny of researchers, its neuronal  
16 architecture has been associated with timing. The anatomy and functional  
17 properties of cerebellar networks have indeed justified neurophysiological models  
18 of cerebellar timing. Cerebellar circuitry is characterized by one sole output, the  
19 Purkinje cells, located in the cerebellar cortex (Ito, 2000), which receive multiple  
20 inputs from granule cells relaying mossy fibres via parallel fibres, and numerous  
21 synaptic junctions from one climbing fibre (Eccles et al., 1967). Early on,  
22 Braitenberg theorized the role of parallel fibres as "delay lines", activating  
23 sequentially different Purkinje cells (Braitenberg, 1961; Braitenberg et al., 1997).  
24 Another model, based on the oscillatory properties of the olivo-cerebellar  
25 network has been proposed (Lampl & Yarom, 1993; Yarom & Cohen, 2002). Olivary  
26 cells, whose climbing fibres project on the Purkinje cells, are characterized by  
27 potential rhythmic sub-threshold membrane oscillations whose apex potentiates  
28 spike occurrence by putting the neuron potentially closer to the threshold (Llinás

1 & Yarom, 1981a; Llinás & Yarom, 1981b; Llinás & Yarom, 1986; Lampl & Yarom,  
2 1993). Oscillations enable the synchronization of clusters of neurons, as revealed  
3 by multiple-microelectrode recordings in rodents (Welsh et al., 1995), or more  
4 recently by dual whole-cell recordings in primates (Turecek et al., 2016). Sub-  
5 threshold oscillations have given rise to the "timing" hypothesis (Ivry & Keele,  
6 1989), which associates cerebellar activity with the temporal relationship  
7 between relevant events. This would entail the existence of a specific cerebellar  
8 timing unit (Ivry, 1997). In other words, the cerebellum would invoke an explicit  
9 representation of time (Ivry et al., 2002), such as equal intervals during an  
10 auditory-paced isochronous finger-tapping task.

11

12 The integration of sensory information with timing function would be the  
13 mechanism by which the cerebellum contributes to AMS. Jacobson et al. (2008)  
14 proposed that, within the cerebellar cortex, there is an association of the  
15 contextual inputs carried by the mossy fibres with a temporal pattern. In other  
16 words, temporal patterns supported by the cerebellar networks would not  
17 necessarily be the byproducts of an inflexible clock, but could be generated "upon  
18 request" (Jacobson et al., 2008). In vivo recordings revealed low threshold and  
19 short latency response of olivary cells to sensory stimulations (Gellman et al.,  
20 1983; Gellman et al., 1985) and also weak periodicity (Lang et al., 1999; Keating &  
21 Thach, 1995; Chorev et al., 2007). Whole cell-recording demonstrates the  
22 correlation between subthreshold oscillation frequencies and the frequencies of  
23 preferred spiking. Khosrovani et al. (2007) revealed the existence of a repertoire  
24 of different neurons characterized by stable frequency settings. These findings  
25 associate different phases of the oscillations with olivary cell discharge, and  
26 consequently legitimize the concept of an internal clock tuned by subthreshold  
27 oscillations. Mathy et al. (2009) proposed to characterize the subthreshold  
28 oscillation phase - axonal discharge relationship with a combination of direct  
29 patch-clamp recordings. A modulation of the relative phase between the synaptic



1 input and the subthreshold oscillations evidenced the dependence of the number  
2 of olivary cells spikes in the phase of the oscillation. Recordings of climbing fibres  
3 from Purkinje cells confirmed their activation by olivary bursts and their role in  
4 triggering plasticity mechanisms. Olivary cell bursts would convey more  
5 information than an on-off state (Najafi et al., 2014; Najafi & Medina, 2013).  
6 Mathy et al. (2009) proposed that the phase dependence of the number of axonal  
7 bursts maximizes the transmission of in-phase information from the olive without  
8 abolishing the out of phase input. Subthreshold oscillations, in addition to their  
9 role as a timekeeping device, would assign a level of saliency to stimulus as a  
10 function of their phase, in-phase stimulus being the most prone to enhance  
11 plasticity mechanisms in Purkinje cells. This mechanism could meet the premises  
12 of both timing, and classical error prediction theories (Albus, 1971; Marr, 1969). If  
13 research now emerges to challenge the cerebellar mapping of proprioceptive  
14 information into a temporal framework during motor learning processes (Kimp  
15 et al., 2014; Yang & Lisberger, 2014), similar experimental evidence of its  
16 contribution to SMS is needed. The synchronous discharge of inferior olive  
17 neurons at a frequency matching those of tremors, following the injection of  
18 harmaline (Llinás & Volkind, 1973), or time locking of Purkinje cells activity to  
19 skilled movements (Welsh et al., 1995), supports the online influence of the olivo-  
20 cerebellar complex on motor control (Lang & Blenkinsop, 2011). The alteration of  
21 motor responses, spinocerebellar reflexes following sensory perturbations, and  
22 Purkinje cells activity in mice lacking electrical coupling in inferior olive cells,  
23 recently highlighted the direct relation between timing of movement and  
24 synchrony of olivary discharges (De Gruijl et al., 2014): the role of the coupling  
25 between olivary cells, which is a condition for their contribution to motor control  
26 (Lang & Blenkinsop, 2011), is not limited to motor learning (as postulated by Van  
27 Der Giessen et al., 2008 e.g.), but seems to have a significant effect on online  
28 temporal processing of sensory information related to motor control.

29

1 The time-pacing ability of cerebellar networks, associated with sensory  
2 integration, still represents a challenge for neuroscientists looking for a functional  
3 definition of cerebellar networks. When reviewing behavioural data, an  
4 agreement on the main contribution of the cerebellum to duration-based timing,  
5 evidenced by the alteration of the timing abilities of the patients affected by  
6 cerebellar lesions (Ivry et al., 1988; Moberget et al., 2008; Grube et al., 2010a), or  
7 disruption of cerebellar function with rTMS (Grube et al., 2010b), was dominant  
8 until recently. But the last beat-based timing protocols extended the implication  
9 of the cerebellum to this type of rhythm. Paquette et al. (2017) used voxel-based-  
10 morphometry, a neuroimaging technique which reveals the relation between a  
11 behavioural variable and gray matter signal (Ridgway et al., 2008), to clarify the  
12 relation between inter-individual variations in gray matter volumes across the  
13 entire brain volume and beat interval discrimination skills evaluated with Harvard  
14 Beat Assessment Tests. The data supported the involvement of the cerebellum in  
15 both beat interval test (BIT) and beat finding and interval test (BFIT), although the  
16 scores of the latter test correlated strongly with gray volume data, whereas the  
17 correlation for the scores of the former test was only marginally significant. If both  
18 tasks require perceiving and producing a gradual tempo change and are  
19 consequently related to absolute timing, the widely accepted function of the  
20 cerebellum, the BFIT, compared to the BIT, adds a beat finding component: this  
21 appears in contradiction with the vision of non-involvement of the cerebellum in  
22 beat perception. The experimental data, in agreement with the compensation of  
23 basal ganglia timing deficits by cerebellar loops in PD patients (see main text), also  
24 legitimizes their contribution to beat based timing. Recent timing models no  
25 longer restrict beat-based timing ability to basal ganglia. Despite the distinction  
26 between neural substrates supporting duration-based and beat-based auditory  
27 timing that Teki et al. (2011b) helped to establish, they subsequently suggested  
28 that neither network may be independent (Teki et al., 2011a). The deficits in both  
29 duration and beat-based timing evaluated in patients suffering from Huntington

1 disease (Cope et al., 2014), which is a pure striatal disorder, support the validity  
2 of this unified timing model (Teki et al., 2011a).

3

4 In sum, there is a general agreement on the existence of some kind of temporal  
5 encoding in the cerebellar granular layer (Manto et al., 2012; D'Angelo & De  
6 Zeeuw, 2009), but a unified model capturing the whole sum of experimental data  
7 is still missing. Measures of performances in cerebellar patients during temporally  
8 non-adaptive (isochronous pacing) and adaptive (tempo-changing pacing) AMS  
9 confirm a global temporal processing dysfunction (Schwartz et al., 2016). The fact  
10 that noticed impairments, which translated into increased asynchronies and  
11 impaired error correction, appeared to be directly linked to the tens-of-  
12 millisecond range preceding the auditory events, reinforced the conception of  
13 Penhune et al. (1998) and Schwartz and Kotz (2013) of the cerebellum as a  
14 structure dedicated to the temporal reduction of time relevant sensory input, i.e.  
15 the encoding of the sensory flow into temporal discrete events.

16

17

## 18 **7.2 Box 3: Motivation, musical pleasure and physical activity**

19 What lies behind the ergogenic benefit of rhythmical auditory stimulations? Other  
20 factors than the underlying dynamical processes reviewed in this article must be  
21 considered. For instance, rhythmical stimulations act as a pain distractor. Directing  
22 attention to music or to a metronome during physical activity may alleviate  
23 unpleasant sensations related to fatigue and pain (Nethery, 2002; Nethery et al.,  
24 1991; Edworthy & Waring, 2006; Karageorghis & Priest, 2012). By focusing on  
25 auditory inputs, people may thus be more willing to push themselves beyond their  
26 mental and physical limits, thereby increasing their running distance as  
27 ascertained by the extra time taken to reach exhaustion. Fritz et al. (2013) clarified  
28 this attentional diversion effect of music by modulating musical agency during a

1 strenuous task which relied on the experience of body proprioception. Because  
2 musical agency significantly decreased perceived exertion, the observed benefits  
3 cannot solely be attributed to an effect of diversion from proprioceptive feedback.  
4 Bigliassi et al. (2017) argued that moderate exercise could promote a combination  
5 of specific mechanisms down-modulating the exercise-related consciousness, i.e.  
6 a reallocation of attentional focus toward auditory pathways, with a concomitant  
7 reduction of communication across somatosensory regions. As a support of this  
8 hypothesis, they reported more positive perceptual and affective responses from  
9 participants when they were listening to music. The down-regulation of the EEG  
10 amplitude at ~700 ms after the onset of muscle bursts corresponded to the  
11 resynchronization time of neurons. According to the authors' interpretation, by  
12 reallocating attention to external influences and dampening fatigue-related  
13 sensations, music would appear to favour more autonomous control of  
14 movements (Bigliassi et al., 2016). These results call for the standardization of  
15 motivational aspects of music when used experimentally. Karageorghis et al.  
16 (Karageorghis et al., 1999; Karageorghis et al., 2006; Karageorghis, 2008)  
17 developed a questionnaire to assess the motivational aspects of musical samples  
18 in the context of physical exercise.

19

20 A glimpse into contemporary hypotheses uncovering the origin of musical  
21 pleasure appears as a prerequisite to deconstruct the satisfaction elicited by AMS.  
22 Musical pleasure would be given through the interplay between prior learning and  
23 changes in the structure of the stimulus (Huron, 2008). The repeated exposure to  
24 a specific style of music, such as Western tonal music, develops our implicit  
25 knowledge of musical rules and regularities, e.g. mental representation of tonal  
26 relationships (Tillmann et al., 2000). When listening to music, the progressive  
27 unfolding of the rhythmical structure, and beats in particular, meet timing  
28 predictions (Bharucha & Stoeckig, 1987), which can be confirmed or violated if the  
29 beat is perceived earlier or later than expected (Rohrmeier & Koelsch, 2012; Bailes

1 et al., 2013; Pearce & Wiggins, 2012). Early on, Meyer (1956) indeed hypothesized  
2 that there was a relation between the degree of expectation fulfilment and  
3 emotion. Acting as a pleasant stimulus, music evokes complex emotions, and the  
4 associated central activations encompass networks involved in memory,  
5 sensorimotor processes, and reward (Blood & Zatorre, 2001; Peretz, 2010;  
6 Pannese et al., 2016).

7

8 Salimpoor et al. (2013) identified the activity in the mesolimbic striatal regions,  
9 especially the nucleus accumbens, as the best predictor of the amount of time  
10 listeners desire to spend on previously unheard music. The activities of auditory  
11 cortex, amygdala, and prefrontal regions were also increased when valuation was  
12 required, but did not appear as a good predictor of reward value contrary to the  
13 functional connectivity of these regions with the nucleus accumbens. As a whole,  
14 ventral striatum (nucleus accumbens) and dorsal striatum (caudate, putamen,  
15 pallidum) appear to contribute respectively to emotion processing derived from  
16 music (Berridge & Robinson, 1998) and rhythm perception and production (Grahn  
17 & Brett, 2007). The interconnection between both parts of the striatum and their  
18 influence by the dopaminergic system represent neuroanatomical clues of the role  
19 of the reward system in associating entrainment with pleasure. If there is no doubt  
20 about the coding of expected reward value by dopamine neurons (Montague et  
21 al., 1995; Schultz, 1998), the activity of single dopamine neurons in awakened  
22 monkeys indicates that they are also involved in coding reward probability and  
23 perceptual salience (Zink et al., 2004; Berridge, 2007; Schultz, 2010): dopamine  
24 neuron activity would code for the precision of prediction error (Friston, 2009),  
25 and would be representative of predictive coding (Schultz, 2016). High-precision  
26 predictions would possess large motivational salience. How this “revisited”  
27 dopamine function fits with the classically admitted role of basal ganglia in  
28 movement selection (Redgrave et al., 1999) is a key question. The control of  
29 dopamine release would optimize proprioceptive predictions, a key determinant

1 of good SMS performance. Based on the interaction between musical appreciation  
2 and prediction error, this still debated theoretical framework could provide an  
3 account for the interplay between SMS and musical enjoyment (see Haile  
4 Gebreselassie's testimony in the 'main text). More generally, this interaction  
5 provides a rationale for the power of music emotional salience, or "groove"  
6 (Michaelis et al., 2014) to elicit movement, as evidenced by its influence on motor  
7 excitability (Kornysheva et al., 2010; Giovannelli et al., 2013; Stupacher et al.,  
8 2013).

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## 1            **9    Figure Captions**

### 2            **9.1    Figure 1. Models of oscillators.**

#### 3            **A. Mechanical oscillators.**

4            a. A simple gravity pendulum experiences sinusoidal oscillations around its  
5            equilibrium point at a constant frequency, with a constant amplitude. Periodic  
6            oscillation is represented by a closed curve in the phase plane.

7            b. The damping of the mass-spring system described here results in the  
8            progressive decay of the amplitude of its oscillations. Biological rhythms are  
9            governed by self-sustained oscillators, which possess a source of energy able to  
10           compensate for the dissipation in the system.

#### 11           **B. Neural Oscillatory processes.**

12           a. The measure of the voltage of a spiking neuron describes periodic variations.  
13           These variations are characterized by an attractive limit cycle in their phase  
14           portrait.

15           b. Phase-response curve (PRC), adapted from Stiefel and Ermentrout (2016), is  
16           when spike time shift is induced by a perturbation of the neuron's voltage ((LOIC  
17           check that this addition of "is" is ok)). The perturbation results in a delayed spike.  
18           The curve describing the PRC is negative before becoming positive: spikes can be  
19           advanced (first half of the cycle) or delayed (second half of the cycle). In the case  
20           of two coupled neurons, the discharge of one neuron can phase shift the spikes of  
21           the other neuron, and vice versa, and deviations from synchrony are corrected.

22           c. Schematic representation of neural oscillators. Neural oscillations can arise  
23           from the interaction between excitatory and inhibitory neural populations (above  
24           adapted from Hoppensteadt & Izhikevich, 1996). Periodic auditory stimuli would  
25           entrain auditory cortical oscillations (below, adapted from Large et al., 2015)  
26           which couple a distributed network of motor and sensory  
27           structures.

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**9.1 Figure 2. Interplay between neural and mechanical activities underlying Auditory Motor Synchronization (AMS).**

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4

**A. Evidence of modulation of cortical activity with auditory stimulations. Sound**

**envelope of an excerpt of music and associated beats (a).** The auditory system

extracts beats as salient perceptual events of a musical piece. **(b) Beat-and metre-**

**related steady-state EPs recorded in a single representative subject** (adapted

from Nozaradan et al., 2011). Nozaradan et al. recorded the

electroencephalogram while participants listened to a musical beat and imagined

a binary or a ternary meter on this beat. Top: the topographical maps of EEG signal

amplitude at 0.8, 1.2, 1.6, and 2.4 Hz, obtained in beat/beat+binary

imagery/beat+ternary imagery conditions. Bottom: the EEG amplitude spectrum

(in microvolts) within a frequency range comprising the frequency of the beat (2.4

Hz) and the frequency of the imagined binary and ternary metres (1.2 and 0.8 Hz,

respectively). In all three conditions, the auditory stimulus elicited, at 2.4 Hz, a

clear beat-related steady-state EP. In the binary metre imagery condition a metre-

related steady-state EP emerged at 1.2 Hz, and at 0.8 and 1.6 Hz in the ternary

metre imagery condition.

20

**B. Dynamical properties of the locomotor chain.** Harmonic mechanical oscillators

are commonly used to model **walking (c: inverted pendulum) and running (f:**

**mass spring system)**. The amplitude of the oscillations depends on the initial

perturbation. Biological oscillators, in contrast, tend to have not only a

characteristic period, but also a characteristic amplitude. In the phase space their

trajectories correspond to a limit cycle. If a perturbation is exerted, they will

automatically come back to their normal behaviour, i.e. to their limit cycle. They

27

1 indeed incorporate a dissipative mechanism to damp large oscillations and a  
2 source of energy to prevent oscillations becoming too small. In **passive walkers**  
3 **(c)** motion is maintained by gravity. Left: after footstrike the swing leg swings  
4 forward past the stance leg until the swing leg hits the ground and a new step  
5 begins.  $\theta$  is the angle between the two legs (adapted from Garcia et al., 1998).  
6 Right: nominal cyclic motion trajectory of the simplest walking model in phase  
7 space (adapted from Hobbelen & Wisse, 2007).

8

### 9 **C. Dynamic entrainment of locomotion to periodic mechanical perturbations**

10 (adapted from Ahn & Hogan, 2012b). Ahn and Hogan applied periodic torque  
11 pulses to the ankle at periods that were different from preferred cadence.  
12 Entrainment occurred when the perturbation period was close to the participants'  
13 cadence, demonstrating the existence of a narrow basin of entrainment, in  
14 agreement with the predictions based on limit cycle oscillators. Entrainment at  
15 both cortical and biomechanical levels exemplifies the possibility to entrain  
16 multiple structures associated with movements. This is so, as long as the external  
17 driving force lies within the basin of entrainment of the biological structure.

18

### 19 **D. Neural Bases of auditory motor synchronization.** Motor areas recruited during

20 AMS tasks mark out the time boundaries of sequentially executed motor actions.  
21 As opposed to the execution of a cueing-free movement sequence, AMS requires  
22 transforming auditory information to extract relevant temporal events regulating  
23 the action. The planum temporale, involved in spectral and temporal analyses of  
24 sounds, projects both to dorsal premotor and prefrontal regions, suggesting a  
25 tight coupling between auditory and motor systems, with input to and from  
26 working memory. Multiple movements are sequenced in SMA and pre-SMA areas,  
27 receiving input from working-memory-related structures, and implementing the  
28 motor command. The functional role of premotor areas is also achieved through  
29 the involvement of cortical outputs to the basal ganglia and the thalamus,

1 connecting both subareas of SMA and the output pathway from the basal ganglia  
2 back to the cortex. The cerebellum contributes to encode the flow of auditory  
3 afferences into motor relevant sensory information. See main text for details.  
4

5 **E. Schematic diagram of the control of locomotion. Adapted from Grillner et al.**  
6 **(2008).**

7 \_\_\_\_\_  
8 \_\_\_\_\_

9 **9.2 Figure 3. Functional connectivity of brain structures during**  
10 **AMS.**

11 **A. Functional link between auditory and motor areas during tapping (Chen et al.,**  
12 **2006).** (a) Manipulating metrical structure during tapping in synchrony with an  
13 external beat, with concomitant scanning of the participants' brain (fMRI). Louder  
14 tones were associated with longer tap durations (b) and concomitant increases in  
15 the BOLD response (c) at auditory (part of the superior temporal gyrus, STG) and  
16 dorsal premotor (dPMC) cortices. This functional connection is supported by  
17 direct connection between posterior STG and PMC, PMC appearing as the relay  
18 for the transmission of auditory information to the primary motor cortex (Chavis  
19 & Pandya, 1976; Luppino et al., 2001; Petrides & Pandya, 2006).

20  
21 **B. Neural correlates of perception vs. perception action during tapping (Chen et**  
22 **al., 2008a).** a. Depiction of stimulus. b. Participants listened in anticipation to the  
23 upcoming tapping task, and then tapped in synchrony with the rhythm.  
24 Activations of the supplementary motor area (SMA), mid-premotor cortex  
25 (midPMC), and cerebellum were found during listening with anticipation. When  
26 participants naively listened to the beat (e.g. without foreknowledge of the later  
27 (LOIC is it later or latter??) tapping task), the same motor regions were activated.  
28 However, in contrast, dPMC - which is sensitive to higher-order information such

1 as the metrical structure - was only engaged during tapping. Ventral premotor  
2 cortex (vPMC) was engaged whenever the sounds were functionally linked to a  
3 motor response, even though delayed. This provides evidence on the  
4 complementary roles of PMC pathways during perception and perception-action  
5 situations (Chen et al., 2009).

6

7 **C. Simultaneous recording of brainstem and cortical electroencephalographic**  
8 **activities during tapping (Nozaradan et al., 2016b).** a. Stimulus: participants,  
9 while listening to a chord - three tones periodically amplitude-modulated inducing  
10 a steady beat - were instructed not to move or to tap on every second beat. The  
11 frequencies spectrum of the stimulus was set to elicit frequency-locked responses  
12 in brainstem and cortical areas. The harmonic chord with partials at 200, 400, and  
13 600 Hz, likely to evoke brainstem nuclei response, was amplitude modulated at  
14 2.4 Hz to induce a beat, prone to elicit a cortical response. b. As expected, cortical  
15 response at beat frequency during sensorimotor synchronization was increased  
16 compared to passive listening. c. brainstem partial steady-state evoked potentials  
17 (SS-Eps) showing enhanced subcortical response in tapping condition compared  
18 to auditory one. d. Spectra of each of the brainstem partial SS-Eps which were also  
19 increased during tapping. For all three types of responses (cortical, brainstems  
20 partials, brainstems sidebands) the increased amplitude in the tapping condition  
21 compared to the auditory condition suggests the contribution of cortical and  
22 subcortical activities modulation in the encoding of sounds during AMS. Brainstem  
23 response enhancement could involve top-down modulation from cortical to  
24 subcortical structures (Bajo & King, 2012).

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### 9.3 Figure 4. Sensory and motor performance during AMS.

#### A. Prestimulus EEG alpha phase synchronicity during a standard auditory “oddball” paradigm (Haig & Gordon, 1998).

a. The synchrony of alpha phase with N100 was measured (ERP, event-related potential arising between 80 and 120 milliseconds after the onset of a stimulus and generated by the primary and association auditory cortices) while listening to predictable auditory sounds. Stimulus consisted in regular tones of 1000 Hz at an interval of 1.3 s. Participants were instructed to ignore these tones and to respond to a second target tone of 1500 Hz which was intermixed with the lower tone by pressing two buttons.

b. In order to clarify the relationship between prestimulus alpha activity and N100 components, the authors proposed the alpha phase synchronicity as a new measure. It corresponds to the circular variance of the alpha phase at stimulus onset across the parieto-occipital sites. Simulated alpha-phase synchronicity (five parieto-occipital sites) at stimulus onset is represented, one with high-phase synchronicity (top) and one with low-phase synchronicity (bottom).

c. Topographic maps showing the group averages of the conventional average N100 amplitude (ERP epochs were conventionally averaged together) and the high- and low-phase synchronicity N100 amplitude (alpha activity phase across the recording sites allowed the identification of high and low synchronicity groups). N100 amplitude was significantly greater in the high than the low phase synchronicity subaverages.

d. Significance probability map (SPM) for the comparison between high- and low-phase synchronicity N100 amplitudes. N100 significantly differed in all 15 sites. The reduction of reaction time in the high prestimulus alpha phase synchronicity cases shows the interplay between external rhythms and brain state related to subsequent stimulus processing.

28

1 **B. Motor activity contributes to sensory selection (Morillon et al., 2014).**

2 a. Experimental protocol and motor-tracking-locked rhythmic gain model.  
3 Rhythmic sequences of 20 pure tones were used. Four reference tones indicated  
4 the beat, followed by an alternation of eight targets and eight distractor tones of  
5 variable frequencies presented in a quasi-rhythmic manner. Targets and  
6 distractors occurred in phase and antiphase with the preceding references.  
7 Participants initially tracked reference beat. They used the reference beat to  
8 maximize the integration of relevant sensory cues while minimizing the relative  
9 weight of irrelevant ones in the sequence of interleaved targets and distractors.  
10 First row: rhythmic motor tracking of musical beats. Second row: references. Third  
11 row: targets in phase with the reference beat. Arrows indicate the temporal  
12 distance between the movement and the target. Fourth row: distractors  
13 presented in antiphase with the reference beat. Arrows indicate the temporal  
14 distance between movements and distractor onsets. Fifth row: gains assigned to  
15 targets and distractors in the model.

16 b. Experimental validation of the model. Target and distractor gains as a function  
17 of their temporal distance to taps (dashed lines stand for the “listen” condition).  
18 The mean frequency of distractors was always equal to the reference frequency  
19 whereas the mean frequency of targets was varying. Participants indicated  
20 whether the mean frequency of targets was higher or lower than the reference  
21 frequency. Sensory gains were estimated for each target and distractor tone using  
22 a multivariate logistic regression of choice against a weighted sum of the  
23 information provided by each tone, expressed in relative distance from the  
24 reference frequency. In the “listen” condition, participants stayed still. In the  
25 “motor-tracking” condition, they performed the task while pressing a noiseless  
26 pad with their index finger in phase with the reference beat.

27 c. Left: categorization performance in the “motor-tracking” and “listen”  
28 conditions. Right: contributions of targets and distractors to the decision in the  
29 “motor-tracking” and “listen” conditions. Overt rhythmic motor activity enhanced

1 specifically the sensitivity to target tones. This effect relies on cyclic fluctuations  
2 in sensory gain time-locked to individual movements. Top-down influences would  
3 sharpen sensory processes, giving sense to the concept of “active sensing”.

4

5 **C. Rhythmic abilities and musical training in Parkinson’s disease (Cochen De Cock**  
6 **et al., 2018).**

7 a. Patients’ individual gait response to various rhythmic stimuli was tested, as well  
8 as their motor and non-motor rhythmic performance. The differences between  
9 patients with positive response and non-positive response to cueing were  
10 examined. The rate of auditory cues was set to be 10% faster than each  
11 participant’s preferred cadence, measured at pretest.

12 b. Individual responses to rhythmic cueing, expressed by the difference in gait  
13 speed between cueing and the baseline, in patients with Parkinson's disease and  
14 in controls. Patients who aligned their steps to the beat also increased their speed;  
15 this was not the case in the controls.

16 c. Beat perception

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1           **9.4    Figure 5. A timekeeper account for the variability of AMS.**

2

3   **A. Phase plane trajectories of the right index during synchronization with a**  
4   **metronome.** One trial consisting in a sequence of 80 stimuli presented with an  
5   inter-onset interval of 800 ms (1.25 Hz). The partial recovering of closed curves  
6   describes a band. Data from Roy et al. (2017).

7

8   **B. Synchronization–continuation paradigm and Wing–Kristofferson two-level**  
9   **timing model (adapted from Wing, 2002).** Participants synchronized their tapping  
10   with the pacing stimuli. During the following unpaced phase (continuation), they  
11   were instructed to continue tapping at the same tempo. Inter-response intervals  
12   (I) are defined by timekeeper intervals (C) and motor implementation delays (M).  
13   Average (I) is matching (C), with variations in (I) reflecting both (C) and (M). The  
14   dashed lines show how negatively correlated (I) (short and long intervals  
15   alternation) can be explained by variation in (M).

1           **10 Tables**

2           **10.1 Table 1. Glossary of basic concepts related to auditory**

3                   **stimulation, gait and dynamical systems.**

Concept	Definition
<b>Rhythm</b>	Regular temporal patterns embedded in music in the form of the alternation of strong and weak sounds, in movements when they are cyclical, or in any temporal series, which exhibit periodicity, such as electrical signals.
<b>Beat</b>	When listening to musical pieces, the perceived beat is the most regularly recurring psychological event in response to a rhythm (Cooper & Meyer, 1960; Large, 2008). More practically, the beat is the regular time interval that we can tap along to when listening to music.
<b>Dynamical System</b>	An ideal model governed by a function which describes its time-dependent evolution, with future states being unambiguously determined (Pikovsky et al., 2003). For example: a simple harmonic oscillator which undergoes sinusoidal oscillations around its equilibrium point (figure 1A).
<b>Oscillator</b>	A system which exhibits rhythm(s). The time-varying amplitude of the variable which characterizes the system (angle of a pendulum, tension in an electronic circuit, membrane potential of a neuron, figure 1 A and B), describes variations about a central value or between different states. Oscillators can be periodic (the time between consecutive corresponding points of the same amplitude is constant: e.g. harmonic oscillators whose output is governed by the sine function) or chaotic. Models referred to in the present review are built upon harmonic oscillators.
<b>Natural frequency</b>	The frequency (number of beats in a unit of time) at which a system oscillates when it is stable and isolated.
<b>Linear vs. nonlinear systems</b>	A linear system of differential equations, defined by affine functions of the variable $x$ , $f(x) = ax + b$ , describes the state of linear physical systems. Nonlinear systems of equations, in which the unknowns are variables of a polynomial of degree higher than

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one, or arguments of a function which is not affine, apply to nonlinear systems behaviour. In a nonlinear system, the solution to the equations is not a linear combination of the unknown variables or functions. The coexistence of many solutions for the same initial parameters is possible.

Within a narrow range of initial conditions and for a short interval of time, a linear equation might describe, with acceptable accuracy approximation, the output of a nonlinear system. The simple swinging pendulum governed by the equation

$$\frac{d^2x}{dt^2} + \frac{g}{L} \sin x = 0$$

(in which  $x$  is the angle of the pendulum from vertical,  $g$  is the acceleration due to gravity, and  $L$  is the length of the pendulum) is a model for the linear oscillator if the term  $\sin x$  is approximated by  $x$ . This is valid for small angles and the numerical solution of the equation is straightforward, the equation now being in the form of a second-order linear differential equation. However, when  $x$  is large, the equation remains in the nonlinear form as depicted above.

**Driven Oscillator**

An oscillator whose position is influenced by an external time dependent force. If the motion of the system is entirely sustained by the time varying force, oscillations are forced.

**Self-sustained  
Oscillator**

In the simplest models of harmonic oscillators, such as a mass-spring system or a pendulum, energy dissipation is neglected. The associated equation of motion predicts the kinetic energy transformed into a potential energy and vice versa, the total energy of the system remaining constant. However dampening mechanisms act against the mass or pendulum motions. If a source of energy compensates for the gradual decay of the movement amplitude, we are in the presence of a self-sustained oscillator. In the pendulum clock the potential energy of the lifted weight is converted into oscillatory motion to prevent the inherent decay of the angle of the pendulum with respect to the vertical. The locomotor system possesses the properties of a self-sustained oscillator as is the case for numerous biological systems such as cardiovascular and respiratory systems.

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<b>Limit-Cycle Oscillator</b>	<p>To describe the state of an oscillator, the value <math>x(t)</math> of its output process is not sufficient since, for a given value of <math>x</math>, the associated function can increase or decrease. A second variable is often called to provide an unambiguous description of the state of the system (Pikovsky et al., 2003). In the case of a pendulum clock, the time evolution of the pendulum angle (<math>x</math>) with respect to the vertical and its angular velocity <math>x'(t)</math> can be used as pairs of coordinates in the phase space, the plot of <math>x</math> vs. <math>x'</math> being the phase portrait. The pendulum clock, which is a periodic self-sustained oscillator, exhibits a phase portrait which consists in superposed closed curves: it satisfies the definition of limit cycle as a closed curve in phase space towards which the trajectories converge.</p>
<b>Resonance</b>	<p>Occurs when an oscillating system is forced to vibrate at its natural frequency. At its resonant frequency, a minimal energy is required to get large amplitude oscillations.</p>
<b>Oscillator Coupling</b>	<p>Coupling between oscillators associates some transfer of energy between them. Two similar clocks on the same support get synchronized due to vibration transmission. Coupling strength describes how weak or strong this interaction is. In the example above, this is determined by the rigidity of the supporting structure and its ability to vibrate ((LOIC is this what you mean?)).</p>
<b>Synchronization</b>	<p>“Adjustment of rhythms of oscillating objects due to their weak interaction” (Pikovsky et al., 2003).</p>
<b>Entrainment</b>	<p>When coupled, oscillators with differing and somewhat close natural frequencies exert a mutual influence on each other. This drives the emergence of a common frequency of oscillation: they are frequency entrained, which can conduct to phase synchronization. However, perfect period and phase synchronization is only one specific case of entrainment. This term also describes partial period and phase adjustment without perfect matching.</p> <p>For a given oscillator, its natural frequency, as well as its frequency associated with the presence of another oscillator, must be measured in appropriate experimental conditions, i.e. with the system to characterize in isolation vs. in specific coupling conditions.</p>

**Neural or brain oscillation** Rhythmic electrical activity observed at different levels of organization, within individual neurons, or within populations of neurons (recorded with commensurate techniques, e.g. with single-unit recording and EEG/MEG respectively). The combination of excitatory and inhibitory activities of different neural populations can give rise to nonlinear neural oscillations (Wilson & Cowan, 1973; Hoppensteadt & Izhikevich, 1996). Neuronal projections can spread oscillations across multiple brain regions. As for any other oscillation, they are characterized by their frequency. Beta waves (13-32 Hz) are modulated by movements in healthy subjects and their suppression is correlated to the predictive value of the cue prior to movement (Gilbertson et al., 2005; Engel & Fries, 2010). It has been proposed that beta activity reinforces postural state at the expense of new movement onset (van Wijk et al., 2012; Doyle et al., 2005; Hammond et al., 2007; Moran et al., 2008). Gamma waves (25-140 Hz) are observed in the sensorimotor areas that are involved during movement (Crone et al., 1998). Motor cortex, as well as subcortical structures (basal ganglia), exhibit transient bursts of high frequency gamma oscillations (60-90 Hz) during movement (Muthukumaraswamy, 2010; Gaetz et al., 2013; Jenkinson et al., 2013). However, on the basis of the irregularity of the gamma phase over multiple oscillation cycles (Xing et al., 2012), Nikolić et al. (2013) proposed that the phase of the oscillation cycle could be locked in a stimulus-dependent manner. The dynamic change of the phase of the oscillation cycle as a function of the spiking activity of neurons preferentially firing for a specific stimulus (Havenith et al., 2011), supports this hypothesis. Globally, action entails event-related beta desynchronization and movement-related gamma synchronization.

**Cadence** Number of steps per time unit (usually minutes) in walking or running.

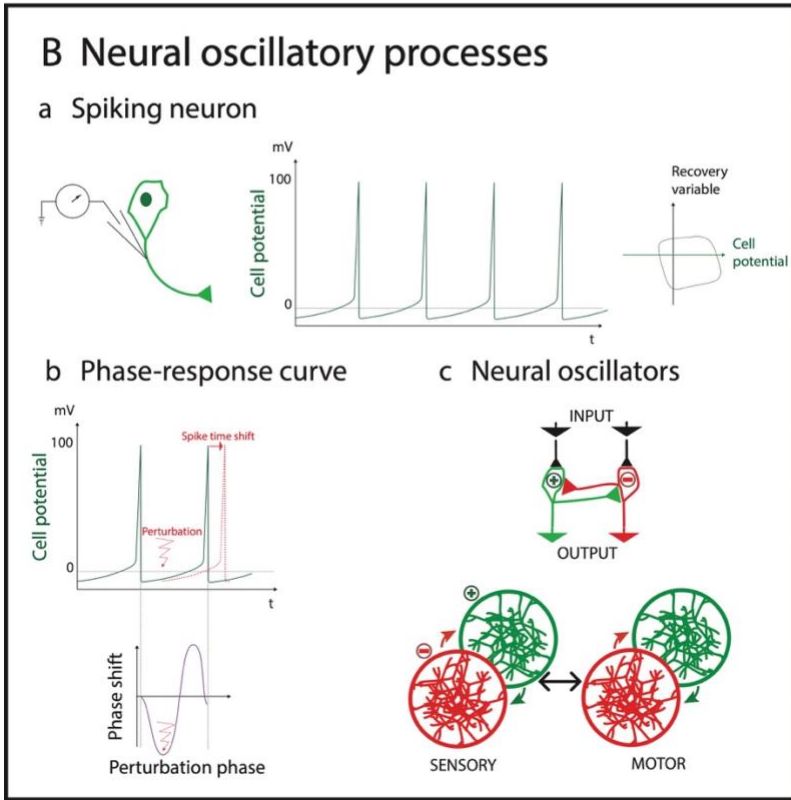
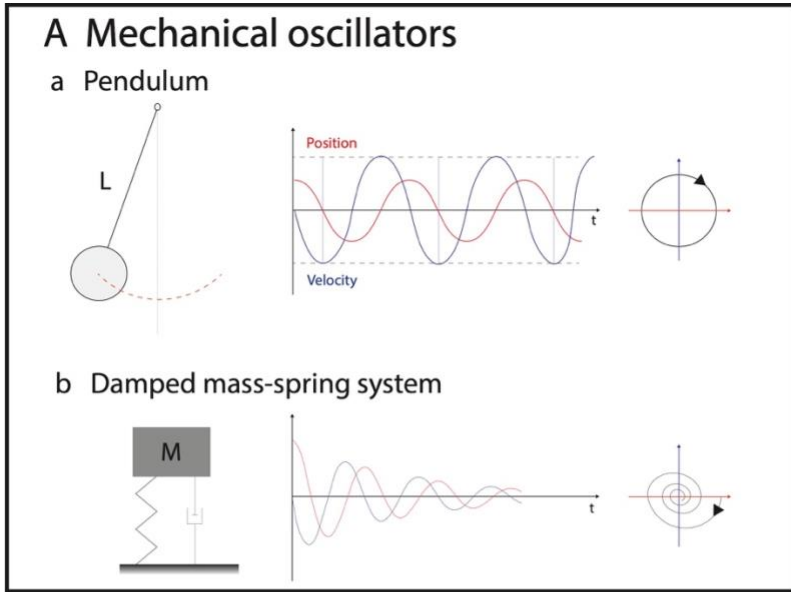
**Running economy** Quantity of energy spent per distance unit during running.

tDCS entails direct stimulation through low current via electrodes connected to the head. Anodal tDCS, which decreases the membrane potential, increases neuronal excitability. Cathodal tDCS, which hyperpolarizes the membrane potential, decreases the excitability of neurons.



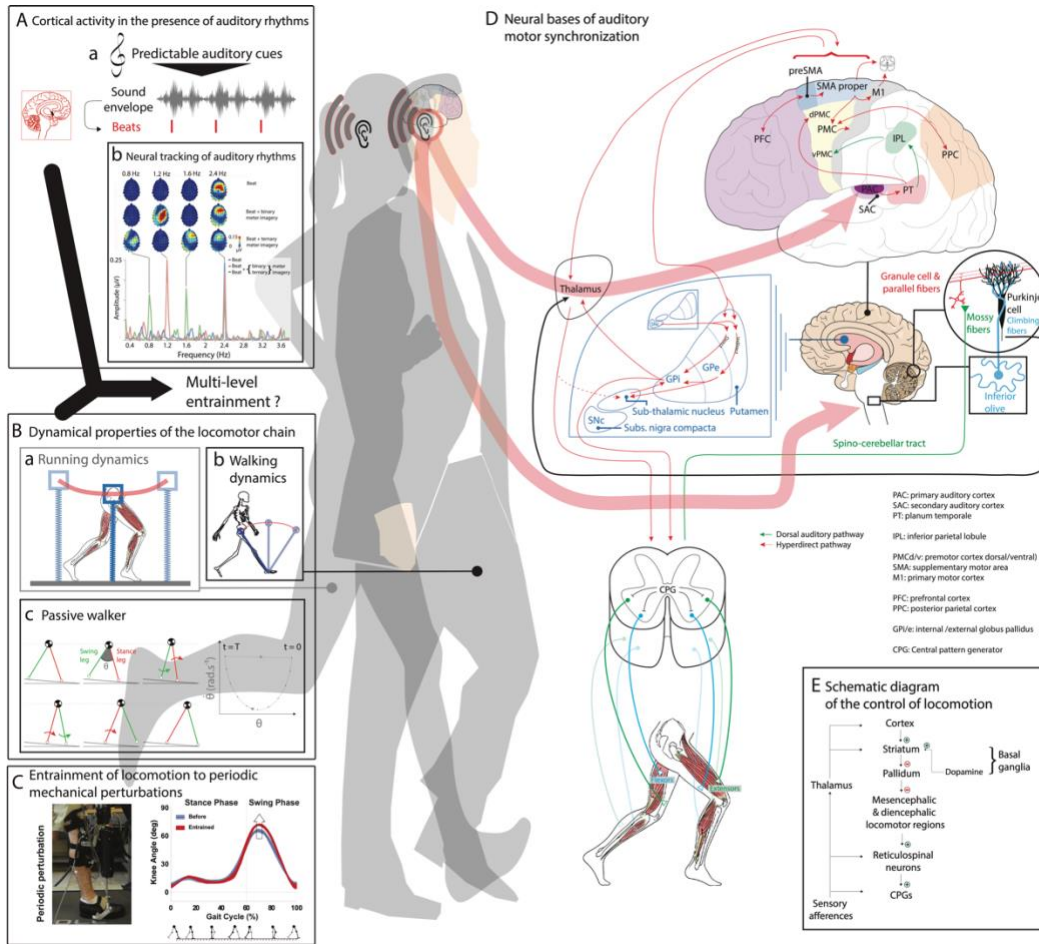
1 **11 Figures**

2 **11.1 Figure 1**



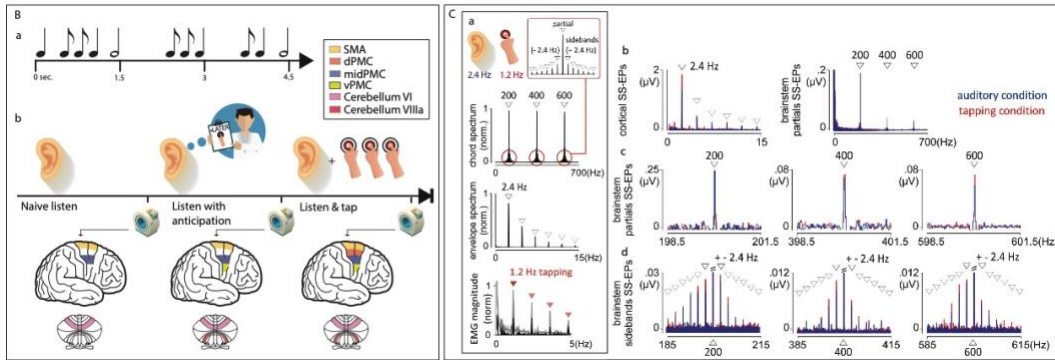
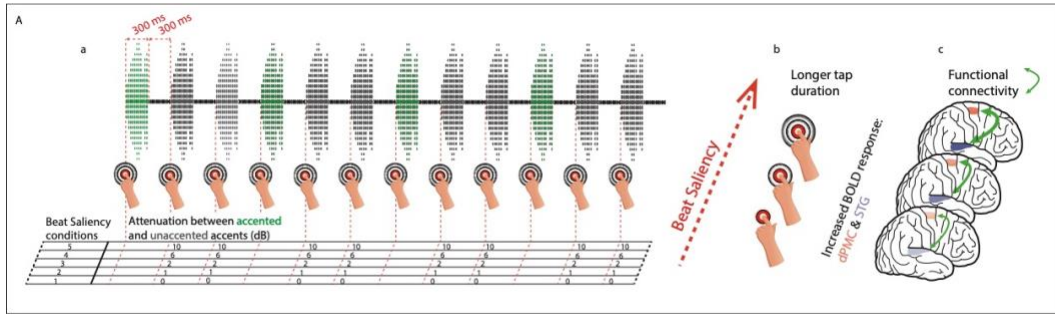
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1 11.2 Figure 2



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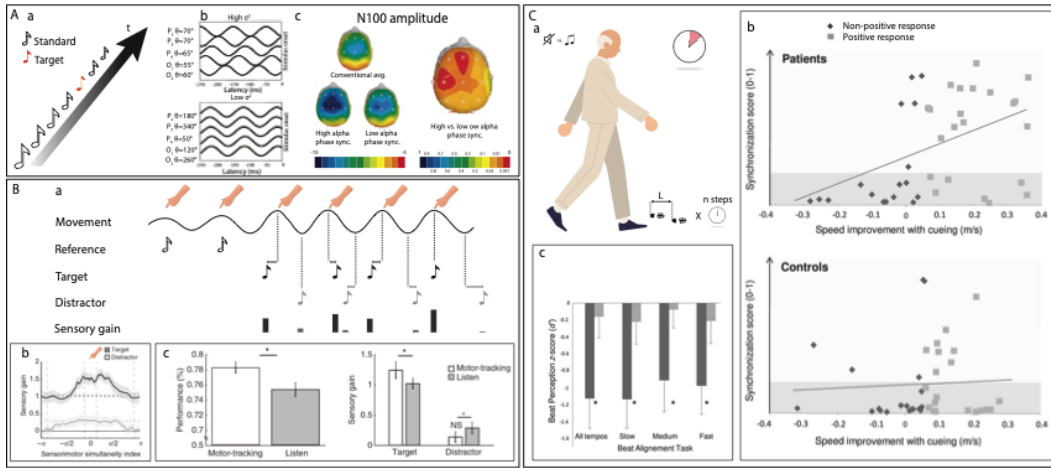
1 11.3 Figure 3



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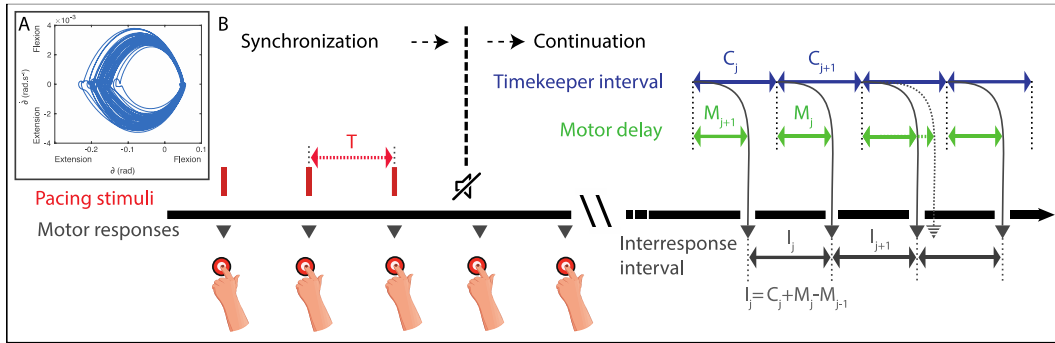
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11.4 Figure 4



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1 **11.5 Figure 5**



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