Rhythmic entrainment as a musical affect induction mechanism

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Abstract

One especially important feature of metrical music is that it contains periodicities that listeners' bodily rhythms can adapt to. Recent psychological frameworks have introduced the notion of rhythmic entrainment, among other mechanisms, as an emotion induction principle. In this review paper, we discuss rhythmic entrainment as an affect induction mechanism by differentiating four levels of entrainment in humans—perceptual, autonomic physiological, motor, and social—all of which could contribute to a subjective feeling component. We review the theoretical and empirical literature on rhythmic entrainment to music that supports the existence of these different levels of entrainment by describing the phenomena and characterizing the associated underlying brain processes. The goal of this review is to present the theoretical implications and empirical findings about rhythmic entrainment as an important principle at the basis of affect induction via music, since it rests upon the temporal dimension of music, which is a specificity of music as an affective stimulus.

Keywords: entrainment; rhythm; music; affect; psychophysiology; feeling

1. Introduction

Music is a powerful form of art, because it is able to elicit strong affective experiences, which may not only result in a brief emotional episode or change of mood in the listener, but may also induce motoric behavioral changes in the form of rhythmic motion or even rhythmic dance movements in a social context. Because of these phenomena, music may even manifest in long-term therapeutic effects (de Dreu, van der Wilk, Poppe, Kwakkel, & van Wegen, 2012; Loewy, Stewart, Dassler, Telsey, & Homel, 2013; Thaut, McIntosh, & Hoemberg, 2015). In fact, this social aspect is believed to play a major role in music, by bringing people together to enjoy or celebrate important events in the community for example. In this sense, music as a social activity promotes common actions between individuals and helps to communicate and even to synchronize actions in a group. Common phenomena include spontaneous synchronization of hand clapping or dancing with the rhythm of the music. Who has not experienced this urge to move with the music when their favorite song comes up? Dance, which is often based on a rhythmic activity in synchronization to the music, has a long tradition in many cultures and across the evolution of mankind (Clayton, Will & Sager, 2005). Moving to music in dance and music listening are thus popular behaviors that seem to be an integral part of our culture. One potential explanation for why such activities are so popular might be that music induces a pleasant state and helps to regulate moods and emotions. Indeed, according to Todd and Lee (2015), these behaviors are intrinsically rewarding and self-reinforcing partly thanks to their stimulation of the vestibular system and its connections with the limbic system. Taking these roles of music together, music can be understood as a social activity that fosters synchronized behavior and stimulates our reward system. This dual role of music raises the question of whether there is a close link between synchronization processes and the affective experiences that music

induces. In this review, we suggest that such entrainment processes play an important role in music performance, as well as in music perception, and that these processes might contribute to the emotional power of music. Specifically, we present four different levels in the music listening context in which such entrainment processes can take place. We describe the subjacent brain mechanisms and discuss the links of these processes to the induction of affective experiences in musical contexts.

1.1. Defining entrainment

Entrainment is the process through which two physical or biological systems become synchronized by virtue of interacting with each other. However, the term entrainment describes not only the case of perfect period and phase synchronization between two oscillators, but also the tendency toward that state that can be observed between two or more systems capable of emitting periodic outputs. Therefore, perfect synchronization is just one specific case of entrainment.

The history of the theory of entrainment can be traced to classical mechanics when Christiaan Huygens first noticed in 1666 that two pendulum clocks set on the same flexible surface would eventually become synchronized (Rosenblum & Pikovsky, 2003). This phenomenon has since been observed between all kinds of devices and organisms exhibiting rhythmic behavior as periodic oscillation. According to Clayton, Sager, and Will (2005), at least two autonomous oscillating systems must be present in order to distinguish entrainment from other concepts. Autonomy means that the oscillators should be able to oscillate, that is, move about an equilibrium position, on their own even when not interacting. In the human body, many physiological processes can be conceptualized as oscillating systems, including cardiac activity,

1 respiration, locomotion, female menstrual cycles, and the periodic firing of neurons. The
2 condition of autonomy is important to differentiate entrainment from resonance, the latter of
3 which is differentiated from the former by its effects being confined to an increase in an object's
4 natural frequency amplitude following exposure to another object with an similar frequency.
5 Moreover, the oscillations of a resonating system cease when the active influence of the original
6 impulse emitting system is removed. However, not all interacting oscillators will entrain, because
7 they need to be relatively close in terms of periodicity for the phenomenon to occur and even
8 then, strict phase and frequency synchronization is not necessarily observed. Entrainment can
9 also occur only at the phase level, that is, phase entrainment or phase-locking; although the
10 frequency may not be modified, we can still talk about frequency coupling or cross-frequency
11 coupling. In cross-frequency coupling, the amplitude of a given frequency (e.g. gamma energy at
12 the cortical level) is coupled to the phase of a lower frequency (e.g. alpha or theta; Canolty &
13 Knight, 2010; Fries, 2005).

15 **1.2. Entrainment with music**

16 Music is a form of art that develops in time. This development is organized into several
17 periodicities for most musical styles. Thus, music constitutes an acoustic signal that often
18 contains different periodicities and therefore can have the properties of an oscillating system at
19 several frequencies. The idea that music can be regarded as an entraining oscillator comes from
20 ethnomusicology, where the effect of especially repetitive music on ritual dancing, including the
21 synchronization of movements and communication between members of a group, has often been
22 studied (Merker, Madison, & Eckerdal, 2009). The most obvious situation of entrainment with
23 music is therefore the adaptation of movements and the production of musical rhythm with the

body, such as hand clapping or swaying. If a musician is playing and producing rhythmical sequences, the musician can both adapt the music to his or her bodily rhythms, for example, to breathing cycles, and, in turn, his or her bodily rhythms can adapt to a chosen musical rhythm, for example, by accelerating breathing. In this case, proper entrainment can take place, since the interaction can work mutually between the musician's body and the music. In the case of music listening, the bodily rhythms of the listener can entrain to the music, but the rhythms of the music are not necessarily influenced. Regarding the definition of entrainment, in this condition, the two oscillators interact only in one direction, that is, asymmetrically. However, this phenomenon is still considered a form of entrainment and is described as such in the literature (Large, 2008), since the rhythms of the body of the listener can adapt their phase and/or periodicities to those of the musical rhythms.

1.3. Investigating rhythmic entrainment as an affect induction mechanism

Rhythmic entrainment has only recently been recognized to play a potential role in affect induction in music listening (Juslin, 2013; Juslin, Liljeström, Västfjäll, & Lundqvist, 2010; Scherer & Coutinho, 2013; Scherer & Zentner, 2001; Trost & Vuilleumier, 2013). The BRECVEMA (brain stem reflexes, rhythmic entrainment, evaluative conditioning, emotional contagion, visual imagery, episodic memory, musical expectancy, aesthetic judgment) framework consists of eight psychological mechanisms that explain how music induces emotions in listeners, citing rhythmic entrainment as one of these mechanisms (Juslin, 2013; Juslin et al., 2010). In this context, the authors claim that “the powerful, external rhythm of the music interacts with an internal body rhythm of the listener such as heart rate, such that the latter rhythm adjusts towards

1 and eventually ‘locks in’ to a common periodicity” (Juslin et al., 2010, p. 621). This adjusted
2 rhythm is then proposed to trigger an emotional response much in the same way that smiling
3 could trigger amusement via proprioceptive feedback mechanisms (Strack, Martin, & Stepper,
4 1988). However, this definition does not clearly state which kind of entrainment the authors are
5 referring to. Their main focus seems to be on entrainment of physiological processes, but they
6 also appear to suggest a mixed concept in which processes of entrainment at the motor and the
7 social levels are elicited via physiological entrainment. A similar process was also proposed by
8 Scherer and colleagues (Scherer & Coutinho, 2013; Scherer & Zentner, 2001) through their
9 peripheral “proprioceptive feedback” route of emotion production (Scherer & Zentner, 2001),
10 later renamed “entrainment and proprioceptive feedback” route in a revised version of the
11 framework (Scherer & Coutinho, 2013).

12 The close link between rhythm and emotions is also illustrated by the central role of
13 prediction and anticipation. By its very nature, rhythmic entrainment generates expectations,
14 explicitly or implicitly, and it is known that dopamine release is indeed related to musical
15 expectations (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011). It could be proposed,
16 then, that entrainment is experienced as a desirable and pleasant state, which would explain our
17 attraction toward activities that require entrainment or why we choose to organize some everyday
18 activities and behavior in a rhythmical way. Musical expectancies are punctual anticipations of
19 musical events to take place. It has been suggested that the confirmation or the disappointment of
20 these anticipated musical events produces an emotion (Meyer, 1956). Rhythmic entrainment is
21 also based on temporal expectancies in time and is therefore a specific kind of musical
22 expectancy. These expectancies can appear in different musical contexts, from the listener’s

1 anticipation of the next drumbeat, to the first violinist's expectation of the director's subtle hand
2 signal.

3 When considering the potential links between rhythmical entrainment and affect, a crucial
4 question is, what kinds of affect rhythmic entrainment could induce. Indeed, affect can be
5 understood as an overarching term that encompasses experiences such as preferences, attitudes,
6 affective dispositions, interpersonal stances, moods, and emotions (Scherer, 2005). According to
7 authors like Russell (Russell, 1980, 2003), all affective experiences may be described in terms of
8 two basic dimensions: "valence" (or "pleasure"), ranging from negative to positive (or unpleasant
9 to pleasant), and "arousal" (or "activation"), ranging from calm to excited (or deactivated to
10 activated). In the context of their framework, Juslin and colleagues (2010) do not specify other
11 affects beyond "general arousal" or "pleasant feelings of communion." However, given the
12 evolutionary origins of synchronous activities (Merker et al., 2009) and their suggested function
13 for the community, it seems reasonable to limit the affective experiences induced by rhythmic
14 entrainment to those that have positive valence, strengthen the feeling of unity with others and
15 promote prosocial behaviors within a group, such as communication, cooperation and
16 coordination (Koelsch, 2010). More specifically, using the emotional dimensions of the Geneva
17 Emotional Music Scale (Zentner, Grandjean, & Scherer, 2008), which was specifically developed
18 to measure emotions induced by music, this could include experiences of wonder, transcendence,
19 tenderness, or joyful activation.

20 In the following section, we will examine the different ways in which entrainment may
21 induce emotions in listeners by expanding upon a framework developed by Trost and Vuilleumier
22 (2013) where entrainment is proposed to occur at four different levels, even simultaneously.

23

2. Levels of entrainment and their role in affect induction

Trost and Vuilleumier (2013) have pointed out that in humans, entrainment behavior can be observed and distinguished on four levels: perceptual, autonomic physiological, motor, and social (see Figure 1). These levels may in fact become integrated and contribute to the emergence of a subjective feeling of entrainment (Labbé & Grandjean, 2014). Although rhythmic entrainment phenomena can be seen as a hierarchical process, the exact form in which these different levels coexist or interact is still being researched. Furthermore, there are many aspects of the link between rhythmic entrainment and affect induction that remain unclear. Using the framework presented by Trost and Vuilleumier (2013) as our basis, we will review the different levels, provide empirical evidence for them from the literature in music psychology and auditory neuroscience, discuss the underlying brain mechanisms involved, and the link with affective experiences. The present review thus aims to describe the different levels in more detail and to present rhythmic entrainment in a more comprehensive manner. First, however, we will discuss the principle of neural entrainment and distinguish it from the other four levels. We make this distinction because neural entrainment is proposed as a general principle of neural communication (Fries, 2005) that is unspecific to music or affect (see Figure 1). Because the main focus of this review is the link between entrainment processes and affect, however, we will mention neural entrainment only briefly. For more information concerning the specific field of neural entrainment and synchronization, we refer the reader to Buzsáki (2006).

2.1. Neural entrainment

Entrainment is a major principle in neurophysiology as a form of communication between organized and connected neurons (Womelsdorf & Fries, 2007). Indeed, cells can communicate

1 not only through the firing of neurons, but also through “communication-through-coherence”
2 (Fries, 2005). The idea is that it is only when neuronal populations are synchronously firing at the
3 same rate and with the same *phase*, (in-phase synchronization), that communication can take
4 place because of the systematic variation of neuronal excitability within a cycle. This is achieved
5 through coupling, which “allows one oscillator to perturb another by altering its phase, its
6 intrinsic period, or both” (Large & Kolen, 1994, p. 10). However, apart from the role of
7 entrainment in neural communication, entrainment is also a mechanism involved in perception ,
8 which can take place at a relatively low level of processing. It is known from single cell
9 recordings in animal studies that neurons can pick up the periodicities of perceived oscillations in
10 a stimulating signal. For example, it has been shown in the tectum of zebrafish larva that neural
11 ensembles can entrain their rhythmic activity to the periodicity of a repetitive sensory stimulation
12 (Sumbre, Muto, Baier, & Poo, 2008). In the auditory domain, studies using LFPs from the
13 primary auditory cortex of primates have provided evidence that neurons can entrain their
14 activities to the periodicity of an auditory stimulation, for example, in the form of clicks
15 presented in the gamma-band range, i.e. 30 Hz and above (Brosch, Budinger, & Scheich, 2002).

16 For humans, one of the most basic levels at which acoustical stimulations can be observed
17 is at the level of the brain stem. Auditory brain stem responses are neural responses that occur
18 within the first 10 milliseconds following the onset of an auditory stimulus. These responses can
19 be measured by using surface electrodes and have been used, among other things, in audiology to
20 detect hearing thresholds since the intensity of simple sounds can be tracked (Mason, McCormick,
21 & Wood, 1988). Evidence that is consistent with neural entrainment has also been found at higher
22 levels of auditory processing in the form of the auditory steady-state response. This describes the
23 phenomenon whereby an increase in the power amplitude of neural responses of neural

ensembles is observed at the frequency of the auditory stimulation. Using intracranial electroencephalography (iEEG) recordings, researchers have shown that auditory steady-state responses can be found at different frequencies (4-16 Hz) in different areas of the primary auditory cortex (Liégeois-Chauvel, Lorenzi, Trébuchon, Régis, & Chauvel, 2004). Similar findings were also reported by using surface electroencephalography (EEG), for example, in a study with children listening to vocal syllables presented at 2 Hz (Power, Mead, Barnes, & Goswami, 2012). Moreover, a study by Will and Berg (2007) on neural synchronization demonstrated how entrainment to regular auditory stimuli could be reflected in the electroencephalogram within the range of human behavior and incidentally, the preferred tempo range in music (60-480 beats per minute; bpm). Intertrial coherence measures showed phase coherence to increase in all frequency bands under periodic stimulation and an entrainment response to occur in repetition rates between 60 and 300 bpm in the corresponding EEG frequency bands (i.e. 1 and 5 Hz). Furthermore, neural entrainment processes can also take place at multiple timescales. For example, when people listen to speech, which is also a rhythmic sequence (in the theta band range, 5 to 7 Hz), theta-modulated gamma oscillations can be observed (Giraud & Poeppel, 2012), indicating so-called cross-frequency coupling.

Neural oscillations and thus also neural entrainment processes have been proposed to be at the basis of all brain activity, including behavior, cognition, and emotional processing (Fries, 2005; Melloni et al., 2007). For instance, concerning emotional processing, Grandjean, Sander, and Scherer (2008) have suggested that it is the neural synchronization between populations of neurons that code for the states of different emotion components that actually results in the emergence of emotional feelings. Elsewhere, evidence suggests that entrainment of the spike timing of neural populations in the basolateral amygdala, a crucial structure in emotion

processing (Murray, Brosch, & Sander, 2014), to hippocampal theta rhythms might mediate emotional memory formation (Bienvenu, Busti, Magill, Ferraguti, & Capogna, 2012). However, defining the exact relation between the lowest level of neural entraining activity and affective experiences is a challenge and is still an issue for research.

2.2. Perceptual entrainment

Perceptual entrainment is defined as the process whereby auditory signals are integrated into a percept of the periodicities in an auditory input. Perceptual entrainment can be regarded as the process that is necessary to perceive periodic information, such as the musical *beat*. Being entrained on the perceptual level creates a conscious or unconscious representation of a periodic rhythmical pattern, which should be distinguished from neural entrainment with regard to the level of processing, even if perceptual representations are rooted in neuronal entrainment. Perceptual entrainment requires an integration of sensory information and top-down influences (e.g. expectations) to form a cognitive representation of the auditory signal, which can be either accessible or inaccessible to consciousness. For perceptual entrainment, a kind of temporal pattern recognition has to take place in order to extract the periodic information contained in the auditory signal, which can happen very fast, as soon as the first couple of beats of the music are heard (Krumhansl, 2000). It is a general principle that when events happen in time with certain periodicities, temporal expectancies are engendered about when the next events are going to happen (for a review see Nobre & Rohenkohl, 2014). The same mechanism is at work in musical rhythms, and thus temporal expectancies are also at the basis of perceptual entrainment. In perceptual entrainment temporal expectancies play an important role as attention is permanently

1 oriented and reoriented in time along the rhythmical structure and in particular along the musical
2 beat.

3 The *beat* in music, which is sometimes also called the *pulse*, is a psychological construct
4 that is perceived because of repeatedly recurring musical events in a specific time interval. The
5 beat can be understood as the basic unit of measurement of evenly spaced events, while the meter
6 “involves our initial perception as well as subsequent anticipation of a series of beats that we
7 abstract from the rhythmic surface of the music as it unfolds in time” (London, 2004, p. 4). The
8 meter in music refers to the temporal organization of beats; it assigns a hierarchy between the
9 beats belonging to one metrical unit by defining a metric for these beats (Lerdahl & Jackendoff,
10 1983). This defined metrical hierarchy allows the distinction between beats that occupy different
11 levels in the hierarchy, which are perceived as being more or less salient. More salient beats are
12 higher in the hierarchy and are often called “strong beats” (i.e. the first beat of a 4/4 time
13 signature), and less salient beats, at lower levels of the hierarchy are called “weak beats” (i.e. off-
14 beat positions, like the second and fourth beat of a 4/4 time signature). A psychological theory
15 that tries to explain the perception of the musical meter in terms of entrainment processes is the
16 Theory of Dynamic Attending (Jones & Boltz, 1989). This theory suggests that the periodicities
17 in a musical rhythm can only be perceived because of entrainment of attentional processes to the
18 different periodicities of the musical meter (Jones & Boltz, 1989). Therefore, the recognition of a
19 periodic pattern and even a metrical hierarchy between the beats presented in metrical music
20 requires cognitive processing and thus constitutes a form of perceptual entrainment, even when it
21 is implicit (Bolger, Trost, & Schön, 2013; Grube & Griffiths, 2009). This implicit perceptual
22 entrainment of attentional processes can be tested in reaction time paradigms. In keeping with the
23 theory of dynamic attending, selective attention is increased in moments of the musical beat, and

1 even more during metrically salient beats, which can lead to increased accuracy and faster
2 processing during these moments. Accordingly, it has been shown that reaction times to visual
3 and auditory targets are significantly reduced when these targets are presented during metrically
4 strong positions with both simple metrical sequences and classical music excerpts (Bolger, Coull,
5 & Schön, 2014; Bolger et al., 2013; Trost et al., 2014).

6 Perceptual entrainment effects can also be explained by predictive coding and predictive
7 timing theories of perception that suggest that our predictions *are* the internal representation of
8 the stimulus (Arnal & Giraud, 2012; Friston, 2005; Giraud & Poeppel, 2012), which is consistent
9 with models of meter perception and particularly with the Theory of Dynamic Attending. These
10 theories suggest that, when a pattern of beats is heard one forms a metrical representation of the
11 rhythm allowing one to anticipate future beats. This representation is then constantly updated as
12 the physical input (rhythm) is compared with the internal prediction (meter), which is corrected
13 as needed, the difference between the two (the “prediction error”) being the only thing that is
14 actually processed by the brain for maximum efficiency (Vuust & Witek, 2014).

15 One example of perceptual entrainment is the phenomenon of *subjective accenting*.
16 Subjective accenting demonstrates that the perception of rhythm is, to some extent, subjectively
17 driven (Bolton, 1894). This phenomenon can be observed when a person is listening to identical
18 isochronous clicks, but perceives a rhythmical pattern or grouping of these clicks instead of
19 identical events, as in the tick tock of a clock, for example. This can even be reflected in greater
20 amplitudes of event related potentials to subjectively “strong” beats in a series of equally spaced
21 and equally loud tones (Brochard, Abecasis, Potter, Ragot, & Drake, 2003; Potter, Fenwick,
22 Abecasis, & Brochard, 2009). Subjective accenting could be explained by resonance theories of
23 rhythm perception (Large, 2008; Large & Jones, 1999; Large & Kolen, 1994), which propose that

1 both the beat and the metrical structure of a piece of music (or any auditory stimulus) emerge in
2 the mind of listeners as internal oscillators with a similar frequency resonate and entrain to the
3 frequencies in the auditory signal. As these oscillators resonate, their amplitudes increase and it is
4 the sum of these amplitudes that then gives rise to an impression of a hierarchical structure. When
5 the auditory stream is an isochronous sequence, it has been proposed that internal oscillators at
6 frequencies close to that of the isochronous sequence but also close to subharmonics of this
7 frequency resonate and entrain, causing a hierarchical structure to be perceived (Bååth, 2015).

8 We also know that a strong sense of both the beat and the meter can be induced through temporal
9 accenting, that is, not necessarily by playing a note louder or softer or even changing its pitch, but
10 simply by manipulating the length of the silences preceding and following a note (London, 2004).
11 In one study, Grube and Griffiths (2009) manipulated both the strength of metrical sequences and
12 the clarity of their endings. Participants reported feeling the pulse most strongly on sequences
13 with more notes during the downbeat (strong sequences), and they accented the last downbeat of
14 a sequence (compact ending) as though it were still playing during the rests until the end.

15 Perceptual entrainment could also be regarded as the underlying mechanism of altered
16 states of consciousness like trance that is induced via listening to repetitive sounds. These trance
17 states can be compared to the experience of flow and are usually evoked to gain insight and are
18 therefore states of high concentration (Hove et al., 2016).

19 A number of studies, using a range of techniques from intracranial and cortical EEG to
20 MEG, have shown evidence for perceptual entrainment and demonstrated how neuronal activity
21 can become entrained to cognitively perceived periodicities in simple rhythms (Fujioka, Fidali, &
22 Ross, 2014; Fujioka, Trainor, Large, & Ross, 2009, 2012; Fujioka, Trainor, & Ross, 2013;
23 Fujioka, Zendel, & Ross, 2010; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan, Peretz,

1 & Mouraux, 2012; Nozaradan, Zerouali, Peretz, & Mouraux, 2015; Snyder & Large, 2005; Will
2 & Berg, 2007). Empirical research in newborn babies in which the researchers used EEG
3 suggests that detecting regularities in auditory rhythmic sequences seems to be innate or learned
4 during the pregnancy (Winkler, Haden, Ladinig, Sziller, & Honing, 2009). This may indeed be
5 the case since the fetus is already exposed to rhythmic auditory stimulations in the womb
6 primarily in the form of the mother's heartbeat. Perceptual rhythmic entrainment is therefore
7 already trained at this early developmental stage, for example, in the context of rhythmic motor
8 actions produced by the mother.

10 **2.2.1. Brain regions involved in perceptual entrainment**

11 Perceiving a rhythm requires aspects of time processing and temporal grouping and it is
12 therefore obvious that brain networks involved in time perception are also solicited in rhythm
13 perception (Geiser, Walker, & Bendor, 2014). These networks have been suggested to include the
14 cerebellum, the parietal and sensorimotor regions (supplementary motor area [SMA], premotor
15 cortex [PMC], and motor cortex), and the basal ganglia (BG; (Grahn & Rowe, 2012; Grondin,
16 2010). Furthermore, it seems likely that the brain processes for perceiving a rhythm without
17 producing any movements would involve brain structures similar to those involved in motor
18 synchronization to music, since the production of a rhythmic movement in synchrony to an
19 external rhythm is supposedly preceded by an internal perceptual analysis. These kinds of tasks
20 refer to the perceptual entrainment level. For example, in a study by Grahn and Brett (2007), the
21 authors found that when participants listened to rhythms without tapping, compared with a rest
22 condition, activations in the SMA, PMC, BG, and cerebellum could be observed. Similarly,
23 Bengtsson and colleagues (2009) demonstrated that passive listening to metrical rhythms, in

comparison to random sequences, activated more dorsal PMC, SMA, and pre-SMA, as well as the lateral cerebellum. Furthermore, when considering whether the focus is on rhythm perception independent of the influence of any motor preparation process, one has to distinguish the studies that include a motor task in any form from those that do not. In a study by Chen and colleagues (2008a), this question was addressed. These authors suggested a distinction in the PMC: the ventral part is involved only in the perceptual task when a subsequent motor response is required. However, a later study reported ventral premotor activations when no tapping was required; in this case, premotor activity increased during the preferred tempo (Kornysheva, von Cramon, Jacobsen, & Schubotz, 2010). In a MEG study on rhythm perception where no motor task was involved, spatial-filtering source analysis also found modulations in the hippocampus, the BG, the PMC, the auditory cortex, the association cortex, and the insula (Fujioka et al., 2010).

2.2.2. Links between perceptual entrainment and affect

A link between perceptual entrainment and affective experiences could imply that sensitivity to the metrical structure increases when an individual listens to music that induces a certain level of arousal or pleasantness. However, thus far, the literature on this relation is limited. One study suggested that consonant music that has been evaluated as pleasant and arousing increased the sensitivity to the metrical structure to a finer-grained level than did dissonant music, which was evaluated as less pleasant and less arousing (Troost et al., 2014).

Furthermore, apart from this first evidence of the link between perceptual entrainment and emotions, a body of work links tempo and pulse clarity with the strength of either perceived or felt emotions and mood in music listening. Tempo and pulse clarity can be regarded as indices of perceptual entrainment: temporal processing is required for both musical features, since it

engenders mental representations of the auditory presentation. It seems an accepted fact that music with a higher tempo induces higher arousal in the listener (Husain, Thompson, & Schellenberg, 2002; McConnell & Shore, 2011). Gabrielson (2009) notes that in emotion recognition studies, fast tempo has also been associated with mostly positive and arousing emotions, such as perceived “activity/excitement, happiness/joy/pleasantness, potency, surprise, flippancy/whimsicality, anger, uneasiness and fear,” whereas slow tempo has been associated with low arousal or even negative emotions such as “calmness/serenity, peace, sadness, dignity/solemnity, tenderness, longing, boredom, and disgust.” However, tempo is determined not just by the speed at which a piece or song is played, but rather by the perceived rate, which is based on the implied pulse, another subjective or at least implied feature. Furthermore, the association of a specific musical tempo with arousal does not imply an association between the strength of perceptual entrainment and the induced affect. Thus, another feature to take into account when considering perceptual entrainment is *pulse clarity* (Lartillot, Eerola, Toiviainen, & Fornari, 2008), which is related to the ease with which listeners can pick up an underlying pulse and thus implies the matching of an internal temporal percept with an external rhythm. Indeed, greater pulse clarity has been shown to be associated with increased “activity” (Luck et al., 2008), that is, arousal, and decreased experienced anger (Eerola, Lartillot, & Toiviainen, 2009). Moreover, a study using continuous emotion evaluations has shown that pulse clarity can also contribute to the prediction of the affective experiences on the arousal but also the valence, i.e. the pleasantness dimension (Trost, Fruhholz, Cochrane, Cojan, & Vuilleumier, 2015). The early sound environment of the womb might be one of the reasons that clear and stable beats are experienced as pleasant. Salk (1962) has suggested that the individual frequency of the mother’s heartbeat would act as a calming influence on the baby. He suggested that the individual heart

1 rate of the mother at rest would lead to an adaptation of the baby's heart beats and that this effect
2 would consequently calm the baby. However, Smith and Steinschneider (1975) demonstrated that
3 generally, only a stable rhythmic acoustic stimulation had a soothing effect on babies. One could
4 argue that this is because rhythmic patterns are more predictable and therefore more easily
5 processed by our central nervous system than arrhythmic patterns, inducing, comparatively, more
6 pleasant states (Winkielman & Berridge, 2003).

8 **2.3. Autonomic physiological entrainment**

9 *Autonomic physiological entrainment* is the tendencies for biological rhythms, which are
10 under the control of the sympathetic and parasympathetic branches of the autonomic nervous
11 system, to entrain to externally perceived rhythms. This form of entrainment includes mainly
12 respiratory and cardiac activity, which are often correlated with each other, but this specification
13 might be due to the difficulty in measuring other visceral activities (e.g. gastric activity). It is
14 obvious that in the case of autonomic entrainment processes, the frequency of autonomic
15 oscillations will not be synchronized to the external rhythm at high frequencies, but that only an
16 approximation can take place, for example, adapting the frequency toward the target tempo or
17 potentially resetting the phase of the autonomic system. Physiological adaptation of respiration
18 and heart rate toward the tempo of the music has often been described in the literature (Etzel,
19 Johnsen, Dickerson, Tranel, & Adolphs, 2006; Khalfa, Roy, Rainville, Dalla Bella, & Peretz,
20 2008; Nyklicek, Thayer, & van Doornen, 1997). Experiments with a simple rhythmical pattern
21 have shown that respiration frequency is adapted in an unconscious manner toward the tempo of
22 the metronome (Haas, Distenfeld, & Axen, 1986). A review by Ellis and Thayer (2010) showed
23 the effective role of slow tempo, especially in dynamically flat and legato music, on reducing the

1 heart rate, respiration rate, and blood pressure. Moreover, several authors have recently suggested
2 that the tempo of the music can have an important impact and that it is even able to predict most
3 physiological reactions in the listener (Etzel et al., 2006; Gomez & Danuser, 2007). Entrainment
4 processes at this level are likely to be relatively slow compared with other levels of entrainment,
5 due to the natural constraints of the cardiovascular system. An example of this can be seen in
6 Bernardi et al.'s (2009) study in which slow endogenous circadian rhythms of about 6 cycles per
7 minute were entrained to phrases of similar length in pieces ranging between 2.5 and 5 minutes,
8 which induced calmness. Because the average respiration rate to pulse rate is 1:4, with the normal
9 respiration rate varying between 12 and 20 respirations per minute and the normal pulse rate
10 varying between 60 and 80 bpm (Lindh, Pooler, & Tampa, 2006), it would take several seconds
11 for entrainment to occur at this level.

12 A potential explanation for autonomic physiological entrainment to the tempo of the
13 music (period entrainment) comes from sports sciences and performing musician studies. Here it
14 has been shown that common and coordinated movements can have a similar entraining effect on
15 physiological rhythms. For example, in choral singing, researchers have shown that cardiac and
16 respiratory efforts become synchronized between the members of the choir and the choir director
17 (Müller & Lindenberger, 2011; Vickhoff et al., 2013). In addition, when individuals do physical
18 exercises, their breathing frequency adapts and thus entrains naturally to the rhythm of the
19 exercise (Bechbache & Duffin, 1977; Paterson, Wood, Morton, & Henstridge, 1986). Moreover,
20 increased locomotion-respiration coupling has also been reported to decrease oxygen
21 consumption, showing that adapting the respiration to movements is a more efficient way to
22 perform (Bardy, Hoffmann, Moens, Leman, & Dalla Bella, 2015). Autonomic physiological
23 entrainment does not necessarily involve the synchronization of movements, but may affect

1 music listeners who sit perfectly still. The non-overt adaptation of the bodily rhythms to the
2 tempo of the music might stem from processes of empathy that make the listener sympathize with
3 the performer of the music and thus synchronize to the imagined or actual movements of the
4 musicians, although these movements might not even be visible (Scherer & Coutinho, 2013).
5 Effects like this are known from studies on sports or rituals (Konvalinka et al., 2011; Paccalin &
6 Jeannerod, 2000).

7 Nonetheless, the power of the musical tempo to have an impact on autonomic
8 physiological processes has been questioned by others. Regarding heart rate, some studies did not
9 find evidence for an adaptation of the heart beat toward the tempo of the music (Dousty,
10 Daneshvar, & Haghjoo, 2011; Koelsch & Jäncke, 2015; Krabs, Enk, Teich, & Koelsch, 2015).
11 However, in these studies, the stimuli included relatively limited tempo variation, tempo range
12 and stimulus duration, which may have biased the results. More research that controls for these
13 issues is needed.

15 **2.3.1. Brain regions involved in autonomic physiological entrainment**

16 Concerning the integration and regulation of autonomic physiological changes in the
17 body, several authors have reported the role of a network of regions, including the insula,
18 cingulate cortex, amygdala, hypothalamus, prefrontal and orbitofrontal cortices, and reticular
19 formation (Benarroch, 1997; Craig, 2009; Karageorghis & Jones, 2013; Thayer & Lane, 2000).
20 Thayer and Lane (2000) have proposed a “central autonomic network,” whose primary output
21 indirectly innervates the heart and the seat of which is the anterior cingulate cortex for the
22 integration of visceral, attentional, and affective information because it receives feedback from
23 peripheral end organs. Moreover, the insula, anterior cingulate cortex, and orbitofrontal cortex

are all involved in processes of interoception (Critchley, 2004); thus, they are also involved in the representation and interpretation of the bodily states and the attribution of an emotional reaction (Critchley, 2005). The insula, anterior cingulate cortex, and orbitofrontal cortex are also known to be involved in the processing of musical emotions (Blood & Zatorre, 2001; Brattico et al., 2016; Koelsch, 2014; Salimpoor et al., 2013; Trost, Ethofer, Zentner, & Vuilleumier, 2012). This double involvement of these regions in the regulation of physiological processes and of emotion processing corroborates the close connection of these processes. It also suggests that these brain regions play a role in autonomic physiological entrainment, which indicates its connections to emotional reactions.

2.3.2. Links between autonomic physiological entrainment and affect

The possible link between autonomic physiological entrainment and affect may stem from the fact that changes in autonomic physiology already form an integral part of the emotion response, and entrainment of autonomic physiological rhythms to the music could therefore trigger an affective response via proprioceptive feedback processes (Scherer & Coutinho, 2013; Scherer & Zentner, 2001). Indeed, researchers have proposed that bodily feelings are essential in emotional feelings (Berntson, Sarter, & Cacioppo, 2003; Damasio, 1996; Friedman, 2010; Grandjean et al., 2008). Feelings are phenomena characterized by the integration of different kinds of representations (appraisals, autonomic reactions, motivations, and motor expression; Scherer, 2005). While the rhythm of the music induces changes in respiration and cardiac activity, these changes might subsequently be interpreted consciously or unconsciously as a felt affective reaction or as being part of the induced feeling (Fancourt, Ockelford, & Belai, 2014). In fact, the notion of rhythmic entrainment as an emotion induction mechanism, as suggested by

Juslin and colleagues (2010), probably stems from this possible link between physiological arousal and emotion, which suggests that there might be a causal relation. On the one hand, one might interpret this as indicating that a slower tempo induces slower respiration or heart rate and that this in turn would induce low arousing emotions, whereas a fast tempo would in the same way induce high arousal emotions. On the other hand, it is known from the literature on chill experiences, which are moments of high musically induced pleasantness (Panksepp, 1995), that physiological reactions are rising in general during the experience of chills, independently of the musical tempo (Salimpoor, Benovoy, Longo, Cooperstock, & Zatorre, 2009). This result seems to contradict the notion of autonomic entrainment as an induction mechanism in the sense that stronger entrainment would be associated with stronger affective experiences. However, this seeming contradiction can be put into perspective if it is assumed that these are two independent processes. It might well be that the chill reaction is a specific kind of affective reaction with no return beyond a certain point, whereas affect induction via rhythmic autonomic entrainment might set in before or after the chill, or might simply be masked by the chill response. Moreover, it has been shown that chill responses to music occur most frequently to familiar and preferred music, and expectations are probably essential in the genesis of such phenomena (Grewe, Nagel, Kopiez, & Altenmüller, 2007; Guhn, Hamm, & Zentner, 2007). Autonomic entrainment has also been shown to be influenced by the level of musical expertise (Bernardi et al., 2009). Autonomic entrainment, in this case, might therefore be associated with a more analytical style of listening, which might be used in the case of listening to rather new and unfamiliar music, which is also less likely to induce chills. Furthermore, autonomic entrainment might serve as an affect induction mechanism such that it adapts the peripheral physiological processes of the listener to the tempo presented in the music and helps to put the listener into the arousal state expressed by

1 the music. In this way, autonomic entrainment influences the peripheral physiological component
2 of the affective response and might therefore be called an induction mechanism.

4 **2.4. Motor entrainment**

5 The phenomenon of motor entrainment to music is the most commonly mentioned
6 example of musical entrainment, for example, in dancing or bouncing, where the musical rhythm
7 is used to synchronize movements. In an evolutionary context, music has been closely linked
8 with dancing behavior or rhythmically synchronized movements as a means of communication
9 and bonding within a group (Merker et al., 2009). Some authors have suggested that it might be
10 an evolutionary advantage to entrain motor actions in time to auditory rhythms, for example to
11 facilitate work (Thaut, Kenyon, Schauer, & McIntosh, 1999) and coordinate movements in a
12 group (Cummins, 2009). Motor entrainment in the form of musical synchronization of
13 movements might therefore be considered a natural human phenomenon, which has recently also
14 been proposed to distinguish humans from other primates (Honing, Merchant, Haden, Prado, &
15 Bartolo, 2012) and which has until recently been thought to be shared only with other kinds of
16 species for whom rhythmic entrainment is a by-product of vocal mimicking learning mechanisms
17 (Fitch, 2009; Patel, Iversen, Bregman, & Schulz, 2009; Schachner, Brady, Pepperberg, & Hauser,
18 2009); this view has, however, recently been contested since evidence for entrainment has been
19 found in at least one nonvocal mimic (Cook, Rouse, Wilson, & Reichmuth, 2013). In contrast to
20 autonomic physiological entrainment, entrainment at the motor level can happen a lot faster,
21 presumably as soon as a clear beat is perceived.

22 In experimental settings, motor entrainment is usually studied as the synchronization of
23 movements in the form of finger tapping to a presented auditory stimulus (for a review, see Repp

1 & Su, 2013; Ross & Balasubramaniam, 2014), that is, asking participants to tap along with an
2 auditory rhythm or music in order to measure the level of synchronization. This task is usually
3 termed sensorimotor synchronization (SMS; Repp, 2005). There are also studies that code more
4 general bodily movements, using video recordings or motion capture systems in order to evaluate
5 the level of motor synchronization with an auditory rhythm or music (Burger, Thompson, Luck,
6 Saarikallio, & Toiviainen, 2014; Kirschner & Tomasello, 2009; Zentner & Eerola, 2010).
7 Furthermore, motor entrainment can be tested more implicitly in a working memory setting in
8 which participants have to reproduce a previously heard rhythmical sequence after a short time
9 interval (Konoike et al., 2012).

11 **2.4.1. Brain regions involved in motor entrainment**

12 To produce a rhythmical sequence, one has to perform actual movements and it is
13 therefore obvious that the entire motor system is involved, including subcortical and cortical
14 motor regions. Functional neuroimaging studies have investigated motor entrainment by using
15 synchronized tapping or rhythm reproduction paradigms to identify the brain regions that are
16 involved: the premotor cortex (PMC), supplementary motor area (SMA), cerebellum, and basal
17 ganglia (BG; Chen et al., 2008a; Chen, Penhune, & Zatorre, 2008b; Grahn & Brett, 2007;
18 Konoike et al., 2012). Studies on SMS that used functional magnetic resonance imaging (fMRI)
19 or MEG techniques showed that a cerebello-thalamo-cortical network is involved in the
20 synchronized beat tapping task that included the sensorimotor cortices, SMA and PMC, as well
21 as the thalamus, posterior parietal regions, and cerebellum (Chen et al., 2008b; Krause,
22 Schnitzler, & Pollok, 2010; Kung, Chen, Zatorre, & Penhune, 2013). In a study that investigated
23 dance movements to music, participants were asked to make dancing steps while lying in the

fMRI scanner, either in synchrony to tango music or to nonrhythmical versions of the same music (Brown, Martinez, & Parsons, 2006); the putamen was found to be significantly more activated during the synchrony condition. Furthermore, the cerebellum has also been suggested to be involved in SMS (Molinari, Leggio, De Martin, Cerasa, & Thaut, 2003; Molinari, Leggio, & Thaut, 2007), because lesions in the cerebellum have been shown to impair precise timing tasks (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). A meta-analysis on the functional neuroimaging literature of audiomotor entrainment suggested a dissociation between externally paced and self-paced tapping (Chauvigné, Gitau, & Brown, 2014); although the cerebellum plays a role in externally paced tapping, probably related to a timing comparison between the external clock and motor actions (Ivry et al., 2002; Molinari et al., 2007), the BG are both involved in externally and internally paced SMS. In other studies, working memory paradigms were used to study how rhythmical information is processed and retrieved in the brain (Grahn & Brett, 2007; Konoike et al., 2012). In a study by Konoike and colleagues (2012), participants had to retain either a rhythmical sequence or a number sequence. The contrast between these two conditions in the retrieval phase shows that for rhythmical reproduction SMA, the inferior frontal gyrus and inferior parietal lobule were specifically involved. Another approach is not to ask participants to tap the beat, but to tap exactly the same rhythm as heard, that is, to reproduce the rhythmical pattern in synchrony (Chen et al., 2008b). Chen and colleagues (2008b) correlated the temporal complexity of the rhythmical sequences and found that the pre-SMA, SMA, dorsal premotor cortex (dPMC), inferior parietal lobule, cerebellum, and dorsolateral prefrontal cortex modulated the activity in terms of the temporal complexity of the presented rhythmical pattern. As was described in section 2.2 (Perceptual Entrainment), the literature seems to suggest that a similar network is involved in the perception and production of rhythms. Some studies have tried to

1 disentangle the roles of the individual brain structures involved in these tasks (Chen et al., 2008a;
2 Grahn & Brett, 2007; Kung et al., 2013). Chen and colleagues (2008a) performed a study in
3 which some participants listened to rhythms without knowing that they would have to reproduce
4 them afterward, whereas others were informed about the tapping task. These authors found that
5 during naïve listening without probable motor preparation, the network recruited was similar to
6 that recruited when the tapping task was announced, which includes the SMA, PMC, and
7 cerebellum. Furthermore, Chen and colleagues suggest that the ventral PMC (vPMC) was
8 involved only when the tapping condition was announced.

9 Several studies have also considered the functional connectivity between the individual
10 brain areas known to be involved in rhythm processing. For example, Chen and colleagues found
11 evidence for functional connectivity between the dPMC and secondary auditory regions (Chen et
12 al., 2008a; Chen, Zatorre, & Penhune, 2006). Moreover, the close interaction of movements,
13 especially to music, might be based on the dorsal stream of auditory processing through which
14 the auditory cortex is closely linked to the motor cortex (Rauschecker, 2011; Zatorre, Chen, &
15 Penhune, 2007). The dorsal pathway of auditory processing projects the signal via the planum
16 temporale and the inferior parietal lobule to the primary and premotor regions (Erickson,
17 Rauschecker, & Turkeltaub, 2016; Rauschecker, 2011; Rauschecker & Tian, 2000). This pathway
18 has also been called the “where” pathway, because it has been demonstrated to be involved in the
19 localization of a sound (Ahveninen et al., 2006; Alain, Arnott, Hevenor, Graham, & Grady, 2001;
20 Kaiser & Lutzenberger, 2003; Kuśmierk & Rauschecker, 2014) and more recently in
21 sensorimotor integration and speech production (Rauschecker, 2012). Kornysheva and colleagues
22 used repeated transcranial magnetic stimulation (rTMS) to specifically test the role of the vPMC
23 as part of the dorsal auditory stream in auditory-motor integration (Kornysheva & Schubotz,

2011). Impairing the left vPMC with rTMS showed that auditory-motor synchronization, that is, tapping to an auditory beat, is compromised, but tapping to a self-paced beat is not. Another study applied rTMS to the dPMC and SMA, but found an impairment of finger movement synchronization to metrical rhythms only for the right dPMC, whereas synchronization to nonmetrical or isochronous beats was intact (Giovannelli et al., 2012). These findings corroborate the important role of the vPMC in auditory-motor integration, which enables accurate timing and movement adaptation to an auditory rhythm.

Finally, another important organ involved in entrainment—and the pleasure we derive from it—likely lies in the vestibular system (Phillips-Silver, Aktipis, & Bryant, 2010; Todd & Lee, 2015). Bharucha, Curtis, and Paroo (2006) mentioned the importance of motion and particularly of self-motion among the conscious recognition of music and affective experiences in the description of conscious music listening experiences. Indirect evidence for this can be seen in a study that examined the effects of motion on meter perception in 7-month-old infants. Phillips-Silver and Trainor (2005) bounced infants to every second or third beat while the infants listened to metrically ambiguous (unaccented) rhythm sequences and found that the infants later tended to prefer (accented) sequences that matched the meter they were bounced to. According to the authors, own-body motion is necessary for this preference to develop because having the infants watch an experimenter bounce did not replicate the findings, pointing to the importance of the proprioceptive and vestibular systems and possibly explaining our propensity to head-bob even when not dancing (Janata, Tomic, & Haberman, 2012). Supported by studies showing that the saccule and lagena of various animals' vestibules are also sensitive to sound, there may be an evolutionary explanation for this link in the vestibular system (Bharucha et al., 2006; Phillips-

Silver et al., 2010), leading Bharucha and colleagues to propose that perhaps in humans, projections from the saccules to spinal motoneurons underlie these tendencies.

2.4.2. Links between motor entrainment and affect

The popularity of rhythmic movement synchronization in music and dance is the most obvious indicator that motor entrainment is tightly linked to affective experiences. Being in synchrony with the music seems to be a pleasant affective state (Janata et al., 2012). The link between motor entrainment and affect has been shown empirically in a study with infants by Zentner and colleagues (2010), in which they reported that the degree of rhythmical coordination of movements to rhythmical music in babies is related to increased displays of positive affect in the form of smiles. Another aspect is that some types of music also seem to comprise the motivational component of the urge to move to the music. This component of wanting to move with the rhythm of the music has also been called “the groove” (Janata et al., 2012; Madison, 2006; Madison, Gouyon, Ullen, & Hornstrom, 2011), which is a term that comes from popular music (Witek, 2009). Janata and colleagues (2012) showed in an experimental study that motor entrainment to the music increases when this music is judged as having more groove. These authors also found that increased motor synchronization leads to more enjoyment, which is further evidence for the link between motor entrainment and affect. Specific features in the music, such as a medium level of syncopation, as well as staggered instrument entrances, seem to increase the experience of groove and in turn the level of SMS with the music (Hurley, Martens, & Janata, 2014; Witek, Clarke, Wallentin, Kringelbach, & Vuust, 2014). Another example that relates motor entrainment to affect is given in states of trance that can be induced by dancing to

1 repetitive rhythmical sounds, inducing altered states of consciousness that are often described as
2 pleasant experiences (Szabo, 2006).

3 A neuroanatomical hint for the close connection between rhythm perception and affect
4 could be given by the fact that both are processed in parts of the BG that are also closely
5 connected to the limbic system. Concerning emotion processing, it is known that the ventral part
6 of the striatum in particular, including the nucleus accumbens, is part of the reward system
7 involved in the processing of highly pleasant emotions (for a review, see Berridge & Robinson,
8 1998). For music, it has also been shown that highly pleasant music involves the ventral striatum
9 (Blood & Zatorre, 2001; Salimpoor et al., 2011; Trost et al., 2012). For rhythm perception and
10 production, however, dorsal parts of the striatum have been shown to play a role, notably the
11 caudate, putamen, and pallidum (Grahn & Brett, 2007). However, given the close connectivity
12 between the different structures of the striatum and the influence of the dopaminergic system on
13 all of them, interactions between these structures might play an important role and may constitute
14 a neuroanatomical reason for rhythmic entrainment as an affect induction mechanism.

15 Blood and Zatorre (2001) found that the activity in the SMA correlated positively with the
16 subjectively rated intensity of chills, which is another indication of an interaction between the
17 pleasantness of the music and the intention of motor behavior. In addition, Kornysheva and
18 colleagues (2010) found that preferred tempo, regardless of rate, determined aesthetic judgments
19 and enhanced ventral PMC (vPMC) activity, which according to them was caused by the
20 propensity towards mimicking one's own preferred tempo (Kornysheva et al., 2010).
21 Interestingly, these authors found a double role of the vPMC, which seems to be important in
22 auditory-motor synchronization, but also plays a role in subjective rhythmical preferences
23 (Kornysheva & Schubotz, 2011; Kornysheva, von Anshelm-Schiffer, & Schubotz, 2011).

1 Finally, certain principles of biological motion in humans are known to guide our
2 appreciation and choice of dynamics in music performance, such as the effect of the final
3 *ritardando*, which strongly resembles the function of a runner's deceleration when stopping
4 (Fleischhaker et al., 2011). Thus, it is possible to envision motor entrainment as an entrainment to
5 kinematic information in the music that facilitates affective responses to living organisms
6 (Derogatis, Lipman, & Covi, 1973) via emotional contagion, for instance (Scherer & Zentner,
7 2001). This is consistent with Bharucha et al.'s (2006) suggestion that experiences of motion are
8 an integral part of the experience of music. It could also explain why motor circuits and the
9 vestibular system, which is crucial for proprioception, are involved when listening to musical
10 rhythms (Trainor, Gao, Lei, Lehtovaara, & Harris, 2009). Furthermore, Bharucha and colleagues
11 have pointed out that "mere synchronization may be a powerful elicitor of emotion" (Bharucha &
12 Curtis, 2008, p. 579), which can be induced by the musical structure itself, but even more
13 important, if the synchronization takes place in a social context, that is, via musically evoked
14 synchronization of movements in a group (Bharucha & Curtis, 2008; Bharucha et al., 2006). This
15 points to the idea that rhythmic entrainment processes in social interactions could be, next to
16 perceptual, autonomic physiological and motor entrainment, another form of entrainment, which
17 also links powerful emotional experiences to synchronization processes.

19 **2.5. Social entrainment**

20 Social entrainment can emerge when listening to or making music together in a group.
21 This is a form of entrainment in a social situation with a musical context, in which the motor
22 actions of two or more people become coordinated in time (for a review on interpersonal
23 coordination, see Keller, Novembre, & Hove, 2014). Social entrainment thus includes

1 interpersonal synchronization, which is characterized by an adaptation of periodic behaviors with
2 another person. Imitating the postures or actions of a partner is a well-known mimicry
3 phenomenon. These imitative actions can then result in synchronized movements such as in the
4 prominent example of synchronized hand clapping in an audience (Neda, Ravasz, Brechet,
5 Vicsek, & Barabasi, 2000). Wiltermuth and Heath (2009) showed that independent of musical
6 activities, acting in synchrony (e.g. walking in step) with partners in a group increased
7 cooperation between the group members. Even seeing or simply hearing the steps of a dyad
8 walking in an in-phase or anti-phase relation, that is, the most stable modes of synchronization,
9 increased judgments of perceived interpersonal rapport (Miles, Nind, & Macrae, 2009). However,
10 by social entrainment, we do not refer to synchronized actions of in-group members, but only to
11 interpersonal synchronization processes in a social context induced by music, for example
12 dancing or making music in a group. Kirschner and Tomasello (2009) showed in an empirical
13 study with children (2 to 4 year olds) that they could synchronize their drumming more
14 accurately with an external rhythm in a social condition, that is, when drumming in the presence
15 of a drumming partner, than when doing the task alone. This finding suggests that in a social
16 context, when playing music in a group for example, the synchronization to a rhythm is
17 facilitated, which also corroborates the Shared Affective Motion Experience model (SAME) of
18 Overy and Molnar-Szakacs (2009). In fact, the SAME model rests precisely on the principle that
19 music is heard as a series of intentional and expressive motor actions and that the synchronization
20 of the above-mentioned networks between performers and listeners leads to “a sense of empathy
21 and social bonding” (Overy, 2012), or, at the very least, to a shared cognitive representation of
22 these acts (Derogatis et al., 1973; Fleischhaker et al., 2011). Hove and Risen (2009) also showed
23 that tapping with a partner in synchrony increased the feeling of affiliation between the partners.

1 Presumably, this is because being in a group and spending time together in a shared activity, such
2 as performing or listening to music as a group, can increase the sensitivity and care for each
3 other, including cooperation and compassion (Valdesolo & Desteno, 2011; Valdesolo, Ouyang, &
4 DeSteno, 2010).

6 **2.5.1. Brain regions involved in social entrainment**

7 Only a few neuroimaging studies have focused explicitly on the aspect of being in
8 synchrony with a musical rhythm within a group. A study by Fairhurst and colleagues (2012)
9 investigated the brain processes of synchronizing finger tapping with a virtual partner, which was
10 in fact manipulated computerized feedback that either gradually adapted to the participant or
11 went out of synchrony with respect to the taps of the participant. The authors found that the more
12 the participants tapped in synchrony with the virtual partner, the more the ventro-medial
13 prefrontal cortex (vmPFC) and posterior cingulate/precuneus were involved. Both of these
14 regions have been reported to be involved in self-related mental representations and in judging
15 one's own or others' actions (Cavanna & Trimble, 2006; Ochsner et al., 2004). Furthermore,
16 these brain regions have been shown to be implicated in task sharing (Sebanz, Rebbechi,
17 Knoblich, Prinz, & Frith, 2007) and prosocial behavior (Rameson, Morelli, & Lieberman, 2012).
18 Synchronized drumming with partners has also been shown to increase prosocial behavior, in the
19 form of spontaneous helping (Kokal, Engel, Kirschner, & Keysers, 2011), and this study showed
20 that the level of prosocial commitment was associated with an increase in activity in the caudate
21 nucleus. In an interactive tapping task with two partners and dual EEG, when the partners were
22 adapting their tapping to each other, there was a suppression of alpha and beta oscillations over
23 motor and frontal regions compared with the condition when the interaction was with a

1 nonhuman computer (Konvalinka et al. (2014). In another study that used EEG, Yun, Watanabe,
2 and Shimojo (2012) investigated how social cooperative interactions influence the
3 synchronization of body movements and neural synchronization. Interestingly, using source
4 localization, the authors found that after a session of social cooperation, the activity in the
5 precuneus increased. Moreover, it was observed that the more participants increased
6 synchronicity of finger movements after the social interaction, the more theta frequency activity
7 was found in the vmPFC. The results of these studies show that social interactions that involve
8 synchronized behavior have a direct impact on brain processes in several areas that are also
9 involved in emotion processing, such as the caudate, the precuneus or the vmPFC (Kokal et al.,
10 2011; Konvalinka et al., 2014; Yun et al., 2012).

12 **2.5.2. Links between social entrainment and affect**

13 From the mimicry literature, it is known that if one's vis-à-vis behaves in the same way
14 that he or she does, this behavior is judged as being more pleasant (Chartrand & Bargh, 1999;
15 Kuhn et al., 2010; Kuhn et al., 2011). This effect, which is also sometimes called the "chameleon
16 effect" (Chartrand & Bargh, 1999), works probably because a person feels understood and
17 accepted by a partner if the behavior is mimicked by the partner, which consequently procures
18 positive feelings. The "chameleon effect" might thus explain why listening and moving together
19 to music can be experienced as being pleasant. In this way, social entrainment adds to the effect
20 of motor entrainment. This additional component of the pleasant experience of social interaction
21 with either another listener or a musician can serve as an additional source of pleasure in the
22 music listening experience. Being in synchrony with the music in a group could be experienced
23 as being more pleasant than being in synchrony with the music alone. When individuals are

1 listening to music in a group and moving in synchrony, they can have powerful affective
2 experiences that are not only induced by the music itself, but also by the experience of being in
3 synchrony with the group (Bharucha & Curtis, 2008; Bharucha et al., 2006), which could also
4 facilitate emotional contagion and empathy effects via motor mimicry and proprioceptive
5 feedback processes (Scherer & Coutinho, 2013; Scherer & Zentner, 2001). As stated earlier,
6 synchronous movements to a musical rhythm in a group or with a partner can induce diverse
7 social feelings, such as an increase in trust (Geeves, McIlwain, & Sutton, 2014; Launay, Dean, &
8 Bailes, 2013), compassion and cooperation (Valdesolo & Desteno, 2011; Valdesolo et al., 2010),
9 or empathy (Koehne, Schmidt, & Dziobek, 2015). Even for children who are 14 months of age,
10 being bounced in synchrony by an adult partner increased the helpfulness of the children toward
11 the partner in a later task (Trainor & Cirelli, 2015). Koelsch (2010) suggested that music
12 performance and listening strengthens several social aspects between group members, such as
13 communication, cooperation, empathy, and coordination. This integrative function of music
14 might therefore explain the attractiveness and prevalence of music in so many cultures. In fact,
15 Phillips-Silver and Keller (2012) suggest that entrainment has two components: a temporal one,
16 having to do with the relationship between the music and the listener's body and brain; and an
17 affective one, having to do with the "mutual sharing of an affective state" (Phillips-Silver &
18 Keller, 2012, p. 1). These authors propose that the latter comes from the pleasure derived from
19 motor entrainment to the music in a social context. In fact, Alcorta, Sosis, and Finkel (2008)
20 suggest that infants likely prefer slow, high-pitched songs with exaggerated rhythms because they
21 probably optimize entrainment between mother and child which, according to these authors,
22 facilitates empathic attachment. This suggestion is consistent with the observation that mothers

intentionally highlight metrical structure through singing and synchronized movements (Longhi, 2008).

3. Discussion

In this review, we have presented a new and more detailed view of rhythmic entrainment and its role as an affect induction principle. We have brought forward four different entrainment levels and discussed their underlying brain mechanisms, as well as their links to affective experiences, which we now summarize briefly. In the following sections, we discuss the potential interrelatedness of the different levels of entrainment and their contribution to a subjective component of entrainment, as well as its role in therapy.

3.1. Key brain regions

Juslin and colleagues (Juslin, 2013; Juslin et al., 2010) suggest that rhythmic entrainment mainly involves “networks of multiple oscillators in the cerebellum and the sensorimotor regions” (Juslin et al., 2010, p. 625) as key brain structures. As we have brought forward in the preceding sections, we suggest instead that the brain regions involved in rhythmic entrainment depend on the level of the entrainment process. However, brain structures that seem to have a key position in rhythmic entrainment are the BG, which play a prominent role in rhythm perception as well as in emotion processing. In fact, in the literature on rhythmic entrainment, the involvement of the BG has been reported on the perceptual, motor, and social levels. We suggest therefore that the BG and the dopaminergic circuits that originate in the BG are the central figures in the connection between rhythmic entrainment and affective experiences. In particular, the BG are able to synchronize and influence the synaptic weights of neuronal populations for

1 generating complex stabilized neuronal networks involved in emotional processing and integrated
2 behavior. Péron and colleagues (Péron, Frühholz, Vérin, & Grandjean, 2013) have therefore
3 proposed that the BG are a crucial component in emotional processing because of the various
4 connections of their different nuclei to cortical and other subcortical areas.

5 However, the BG are just part of a network of brain regions that are involved in
6 entrainment processes. Depending on the level of entrainment involved, motor circuits, frontal
7 cortical regions, parietal cortical regions, or the cerebellum might interplay to produce
8 synchronies.

10 **3.2. Induced affect**

11 In terms of the expected affective experiences, we believe that rhythmic entrainment is
12 mostly involved in the induction of both high and low arousing *positive* emotions, since pieces
13 that are characterized by a slow but regular pulse, such as slow waltzes or lullabies, can have a
14 pleasant calming effect and be equally effective in inducing a pleasant sense of regularity and
15 motion as pieces with a fast tempo. Janata et al. (2012), for instance, found a positive relation
16 between participants' inclination to move and their enjoyment of low, mid, and high "grooving"
17 songs, the latter inducing the greatest amount of body movement (groove being defined as "that
18 aspect of the music that induces a pleasant sense of wanting to move along," p. 56). Therefore,
19 entrainment could be predicted to induce more complex affective experiences, including musical
20 emotions such as peacefulness, but also power and joyful activation, for example (Zentner et al.,
21 2008). Moreover, regarding the level of social entrainment, it has been reported that social
22 synchronization processes can induce different kinds of prosocial interpersonal dispositions and
23 affects, such as trust (Launay et al., 2013), compassion, and cooperation (Valdesolo & Desteno,

2011; Valdesolo et al., 2010). A study on self-reported experiences of entrainment found that two different factors underlying “subjective entrainment,” the feeling of wanting to move (motor entrainment factor) and the sensation of having one’s inner rhythms change (visceral entrainment factor), significantly predicted different aesthetic emotions (Labbé & Grandjean, 2014). Other possible outputs, distinct from both mood and emotions, are pleasantness and liking. Concerning pleasantness, we submit that the process of being and feeling entrained is a pleasurable experience in and of itself that is born of our predisposition toward entrainment. On the other hand, liking, which may be understood as an affective *preference* (Brattico, Bogert, & Jacobsen, 2013; Brattico & Pearce, 2013; Juslin, 2013; Scherer, 2004), supposes the involvement of an evaluation or *aesthetic judgement*. This judgement is made on the basis of a series of personal or cultural aesthetic criteria such as beauty, skill, or expression, for example (Juslin, 2013). If a particular performance of a musical piece, song, or rhythm is judged as being “good” or “bad” it may result in preferences such as liking or disliking, respectively. As mentioned earlier, evidence shows that music that grooves more is liked better (Janata et al., 2012); therefore, the groove or how entraining the music is found to be could be an aesthetic criteria for many people. However, if a performance is judged as being extraordinarily good or bad, such aesthetic judgments might themselves lead to full-blown emotions (Juslin, 2013).

3.3. Relationships between levels of entrainment

As pointed out in the Introduction, the relation between different levels of entrainment and their interaction is still an issue for research. Thus far, only a few studies have shown a link between the different entrainment levels. First, regarding the neural and the motor levels, increased tapping accuracy to an external beat is associated with less variability in auditory brain

stem responses (Tierney & Kraus, 2013). Some evidence has also shown that the perceptual and the motor levels seem to interact. Moving to an auditory beat increases the accuracy of time interval judgments (Manning & Schutz, 2013) and the accuracy of motor synchronization is positively related to the entrainment of attentional processes, measurable by neurophysiological EEG signatures (Schmidt-Kassow, Heinemann, Abel, & Kaiser, 2013).

Given that only a few empirical studies have focused on rhythmic entrainment and its role in affect induction, the links between the levels remain to be further explored. From the different literature and domains, it might seem that there is little relation between the different levels of entrainment described here. However, we will now borrow an approach used to conceptualize emotion in order to illustrate that such links may in fact exist. Currently, many theorists agree with a multicomponential view of emotion (Moors, 2007; Moors, Ellsworth, Scherer, & Frijda, 2013), that is, that emotions comprise several components such as action tendency, bodily responses, and emotional experience. According to the Component Process Model (CPM) of emotion (Scherer, 2005), there are at least five (cognitive, motivational, neurophysiological, motor expression, subjective feeling) and though each is associated with a different function they are all highly interrelated; changes in one produce changes in the others. In fact, in this framework, it is the synchronized responses of these different components that constitute an emotion. Similarly, it could be proposed that the different levels of entrainment constitute the components of a similar, single unified process. If this is the case, then changes at one level could trigger changes at another, even without listener's awareness. Indeed, in the CPM the feeling component has the special role of integrating and regulating the other processes, but this central representation involves aspects that do not all necessarily enter awareness (Grandjean et al., 2008). Much in the same way, it could be that we *feel* emotionally affected or entrained by music

(Labbé & Grandjean, 2014) or find a song “groovier” than another (Janata et al., 2012) without being able to pinpoint why. Conversely, we can find ourselves tapping our feet to the beat without even realizing what we are doing or how it is affecting us.

Thus, we propose that instead of separate independent processes, different levels of entrainment are components of the same phenomenon that can be measured in different ways, all of which can have an impact on the listener’s subjective feeling component. Philips-Silver and Keller’s “affective entrainment” component certainly seems to support this view because it is based on the interdependence between social entrainment—being in time together—and motor entrainment—being in time with the music. As with emotion, perhaps tapping into one level of entrainment triggers the others. The results of Philips-Silver and Trainer’s (2005) bouncing experiment seem to support this idea because own-body motion was necessary to develop the preference for accented sequences.

3.4. Directionality

Another general aspect that is of importance when studying and questioning the role of rhythmic entrainment as an affect induction mechanism is the directionality of the relation. The studies from the literature that test the level of rhythmic entrainment with a certain affective state (affect → entrainment) should be well distinguished from other studies that test the affective reaction, given a certain state of entrainment (entrainment → affect). In fact, since this link has not yet been the subject of many studies, the directionality between induced affect and rhythmic entrainment has not been studied in detail. For example, one study investigated the direction from pleasant music leading to increased perceptual entrainment (Troost et al., 2014) by testing how pleasant music would entrain attentional processes to the meter of the music. Janata and

colleagues (2012) showed that spontaneous motor entrainment to the music increases when this music is judged as having more groove. In a different study investigating the opposite direction, self-reported ratings of subjective entrainment were found to significantly predict the intensity of mostly positive musical emotional dimensions, showing that the more entrained listeners feel, the more likely they are to experience positive emotions (Labbé & Grandjean, 2014). Thus, the causal direction in this association remains unclear. More research is needed to formally test the directionality between induced affect and entrainment processes. It is likely that entrainment itself, for example, at the motor level, would induce a kind of dynamic virtuous circle, together with the external musical rhythms, and would then also contribute to reported feelings related to music. Or, it is also possible that the link between affect and entrainment is a bidirectional cyclic phenomenon, where both, the affective reactions as well as the entrainment processes facilitate and foster each other. It could be that the effects of entrainment on affect and especially emotion are in fact an interaction effect between low-level bottom-up processes (afferent feedback) that eventually combine with top-down (efferent) responses leading to a unified response (e.g. Schachter & Singer, 1962).

3.5. Rhythmic entrainment in therapy

In regard to the application of rhythmic entrainment, it should be acknowledged that rhythmic entrainment and its effect on affect can be directly implemented in therapy. In particular, in patients with movement disabilities, rhythmical exercises that are based on entrainment can be beneficial. Interesting examples of pathological motor entrainment come from studies with Parkinson patients. Several studies have shown that listening to or watching rhythmical patterns can help diminish the symptoms in these patients, who are usually impaired

1 in initiating movements, especially in gait, because of degeneration in the substantia nigra, which
2 is strongly connected to the different nuclei of the BG (del Olmo & Cudeiro, 2005; Derogatis,
3 Rickels, & Rock, 1976; Pacchetti et al., 2000; Schwartze, Keller, Patel, & Kotz, 2011). Rhythmic
4 auditory stimulation to facilitate gait has been successfully applied in Parkinson patients
5 (McIntosh, Brown, Rice, & Thaut, 1997; Thaut & McIntosh, 1999), in patients during recovery
6 from a stroke (Thaut, McIntosh, & Rice, 1997), and in patients with spinal cord or traumatic
7 brain injury (de l'Etoile, 2008; Hurt, Rice, McIntosh, & Thaut, 1998). Schwartze and colleagues
8 (Schwartze et al., 2011) showed that patients with focal lesions in the BG had difficulties in
9 adapting their movements to tempo changes (*accelerando* and *ralentando*) when asked to tap
10 along with the tempo of a rhythmic sequence. Furthermore, for perception only, researchers have
11 shown that Parkinson patients are also impaired in discriminating beat-based rhythms (Grahn &
12 Brett, 2009). Moreover, music therapy that involves passive listening as well as active motor
13 involvement, and thus entrainment processes, has beneficial effects not only on the motor
14 symptoms, but also on the emotions of Parkinson patients (Pacchetti et al., 2000), which further
15 speaks to the potential role of the basal ganglia in linking entrainment and emotional responses.

16 Entrainment-based musical activities can improve various outcome measures in elderly,
17 nonclinical populations as well. A specific kind of musical activity that is built on the idea that
18 music is taught through movements is the Eurhythmics of Jaques-Dalcroze (Jaques-Dalcroze,
19 1919). Regular Dalcroze Eurhythmics exercises reduced not only the risk of falls and gait
20 variability in elderly participants, but also anxiety (Trombetti et al., 2011; Hars et al., 2014).
21 Moreover, Dalcroze Eurhythmics can also be beneficial in clinical populations, such as patients
22 with autism or post-traumatic stress disorder (Berger, 2016).

Given the theoretical and empirical evidence for rhythmic entrainment as an affect induction mechanism, it seems likely that rhythmic entrainment processes at different levels constitute the crucial element of the therapeutic effect. One of the underlying mechanisms of this therapeutic effect definitely seem to be constituted by the emotional power of music, which increases the pleasantness, the motivation, and the compliance of the patient to maintain a certain training intervention. But there are also other underlying mechanisms that are intrinsic to entrainment processes, which would support the therapeutic effect of music- and rhythm-based interventions. First, entrainment of attentional resources on the perceptual level would lead to an increase of attention and an enhanced processing of information in punctual moments (Bolger et al., 2013). Second, entrainment on the autonomic physiological level, such as respiration cycles could lead to a reduction of effort to perform physical exercises (Hoffmann, Torregrosa, & Bardy, 2012). Third, entrainment on the motor level would facilitate the movements (Thaut et al., 1997), and fourth, even more so when the exercises have to be performed in a group (Kirschner & Tomasello, 2009). Assuming that rhythmic entrainment procures and fosters also positive feelings and pleasant emotional states, it seems that entrainment-based musical activities could constitute altogether a sensible and effective intervention for clinical and nonclinical populations.

4. Conclusion

We have reviewed and discussed different aspects of rhythmic entrainment as an affect induction mechanism by reviewing the literature and describing the reported entrainment phenomena. We noted that different phenomena are described as rhythmic entrainment, all of which have a common basis but differ in their level of expression, and therefore we suggested that differentiations should be made between the different phenomena (neural, perceptual,

1 autonomic physiological, motor, and social) in order to identify the processes more precisely
2 (Figure 1). Regarding these different forms of rhythmic entrainment, although quite different
3 phenomena are presented, what they have in common is that the music triggers synchronization
4 behaviors in different biological rhythms and this tuning into the periodicities of the musical
5 rhythms has an affective component. Apart from the neural level at which neural ensembles
6 synchronize, which seems to be at the basis of all entrainment effects, all other forms of
7 entrainment have been described as involving a kind of affective experience. For example, when
8 faster respiration leads to higher felt arousal, moving in synchrony to the rhythm of the music
9 feels pleasant and sharing the same musical experience in a group creates the positive feeling of
10 acceptance and integration. For these reasons, the close relation between musically induced
11 rhythmic entrainment and affective experiences has become of increasing interest in music
12 psychology. More research is needed to further investigate the notion of rhythmic entrainment as
13 an affect induction mechanism.

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Figure captions

Figure 1. Diagram of the rhythmic entrainment levels and the relationship between them.

Neuronal

- Coupling of neurons
- Communication through coherence

Perceptual

Perceptual representation of periodic rhythmical patterns, e.g. 'beat' or pulse' perception

Autonomic physiological

Adaptation of physiological rhythms towards the musical tempo

Motor

Sensorimotor synchronization with the beat and meter

Social

Musically driven synchronization of behavior with conspecifics

Subjective

Subjective representation and experience of entrainment