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Music listening as adaptive behaviour: Enaction meets neuroscience

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Background in musicology. This paper sketches the recent disciplinary history of musicology, stressing the shift from a disembodied and detached approach to the musical structure to an approach that takes the human listener as a starting point. It discusses the role of embodied cognition and the role of enactive models for the study of the way how listeners cope with sounds, relying to some extent also on the phenomenological approach of "music as heard" and "music as experienced" that was advocated already in the 1980s.

Background in cognitive science and neuroscience. The enactive approach, as applied to music, is part of the emerging field of 4E cognition, which is an umbrella term for embodied, embedded, extended and enacted cognition. It is elaborated in this paper, more in particular its relations with the sensorimotor approach to music cognition, and is brought in relation to neuroscience, which has been seen as opposed to the embodied approach, due to its detached and disembodied conceptions of mental computation and representation. This has been challenged by more dynamic approaches in music and brain studies, as exemplified in the contributions from neuroaesthetics, neuroplasticity and brain connectivity studies as applied to music.

Aims. The major aim of this paper is to bridge the gap between a disembodied and detached conception of neuroscience and recent developments in cognitive science, that take an enactive and embodied view to music cognition.

Main contribution. This paper is an overview and programmatic paper. Starting from the inner/outer distinction in the philosophy of mind, it first delves into the position of the enactive approach within the broader field of embodied cognition, stressing also the role of the sensorimotor approach and action and perception studies. It then sketches the possible contributions from the neurosciences to the enactive approach to dealing with music, revolving mainly around the concepts of neurodynamics, neuroaesthetics and neuroplasticity and the conception of music listening as adaptive behaviour. It is argued that the emerging field of connectomics, which studies the networks of the brain, may play a crucial role in understanding some of the underlying mechanisms of musical experience.

Implications. The major implication of this paper is the emphasis it puts on a dynamic and ongoing description and assessment of the musical experience. It provides an overview of existing techniques for empirical testing as well as possible new directions for future research. Central in this is the dynamic approach to music cognition and the search for a kind of real-time and ongoing mapping between the sonorous articulation and the lived experience by the listener.

Keywords: music listening, embodiment, enaction, adaptive behaviour, neurodynamics, neuroaesthetics, neuroplasticity, connectomics

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Musicology as an autonomous area of inquiry has a rather young history. It has been established as an academic discipline around the second half of the 19th century by Adler (1885) who proposed a subdivision in *historical*, *systematic* and *comparative* musicology. The systematic approach was conceived as joint discipline that comprised both systematic and comparative aspects to study the organization of musical structures in a transdisciplinary and cross-cultural approach (Schneider, 2008a). The "systematic approach" envisioned a specific and effective approach which can be equated with sophisticated, thought-out and well-organized procedures of thinking as opposed to arbitrary, inconsistent access to observations; the "comparative approach," on the other hand, intended the possibility to order objects, structures and elements in relation to each other by studying them systematically concerning their distinctive features and by relying on classifications that are based on categories of identity, difference and variety (Elschek, 2008). Though Adler's system was originally meant as a universal model to encompass both existing and established fields of research as well as envisioned ones, the historic and systematic branches evolved quite quickly in different directions, due partly to their different methodology: the historic methodology relies mainly on philological skills, descriptions, musical analysis, hermeneutic understanding and interpretation; the systematic methodology instead relies on measurement, experiment or empirical investigations, data analysis, statistics and modelling. The two disciplines, therefore, can be termed distinctly as being either *historical-philological-hermeneutic* or *scientific-experimental-comparative* (Schneider, 2008b).

Since these early days, musicology has continued to evolve and its disciplinary history is characterized by multiple attempts to broaden its scope with new fields such as cognitive musicology, computational musicology, empirical musicology and many others. Many of these attempts, however, have taken a rather disembodied stance towards music. As such, a new field of research has emerged over the past decades which proposes embodied and enactive models for the study of the way how listeners cope with music as it sounds (Reybrouck, 2021). There have been already promising attempts in the 1980s, which revolved around the conception of "music as heard" and "music as experienced", conceiving of music as something that has existential structure and meaning (Lochhead, 1986; Clifton, 1983), echoing somewhat the claims of early philosophers such as Aristoxenus, who approached music primarily as an experience rather than an object (Bonds, 2014). In this view, actual involvement with music exists in experience, rather than in reason and interpretation (Reybrouck, 2014, 2017a, 2017c; Reybrouck & Eerola, 2017). Or as Jankélévitch has put it: our involvement is *drastic* rather than *gnostic* (Jankélévitch, 2003; see also Abbate, 2004). The consequences of this approach, though, are considerable: they question the status of the score, the role of our theoretical notions about music and the analytical methods to be used to study the music as a sounding phenomenon.

Following this phenomenological approach, a distinct field of research has emerged over the past decades which proposes embodied and enactive models for the study of the musical mind. This approach relies mainly on an understanding of the self-organizing aspect of cognition, which can be described as an ongoing process of dynamic interactivity between an organism and its environment (Cox, 2016; Clarke, 2005, Leman, 2007, Lesaffre et al. 2017).

The question can be raised here about the position of the *neurosciences* in this emerging field. The last decades have seen an overwhelming bulk of contributions from this field (see Reybrouck et al., 2018b for an overview), but they have been criticized somewhat for holding computational and representational positions concerning the study of music. Music processing, in many of these studies, remains enclosed within the brain with no connections to the real world and with musical sense-making being explained in a somewhat detached and disembodied way (see Kiverstein & Miller, 2015; Schiavio et al., 2017a; Thompson, 2007). Such an approach is exemplary of the inner/outer dichotomy that draws a dividing line between what goes on in the head and the world, as exemplified most typically in Fodor's "language of thought" hypothesis (Fodor, 1975), and in what is commonly defined as "good old-fashioned artificial intelligence" (or GOFAI) (see Haugeland, 1985). It is an approach that has been recently challenged in the sense that the actual living experience of music cannot be restrained by pre-given processing programs in the skull (Chemero, 2009, and Schiavio et al., 2017a for musical applications). What is needed, on the contrary, is a "brain-body-world nexus" (Schiavio & Altenmüller, 2015). Musical sense-making, then, is not to be considered in terms of static representations – as something that is petrified in a virtual world outside of the actual time of sounding – as exemplified typically in the concept of the *musical work* with its reliance upon the score, compositional or authorial control, with the possibility of repeatability, the notion of permanence, and the emergence of aesthetic autonomy (Goehr, 1992; Moran, 2014, Steingo, 2014). Rather, it should be conceived as a dynamic and continuous interplay with the environment. This is a conception that is indebted to recent contributions in the mind sciences, with findings from embodied cognitive neuroscience (Dotov, 2014; Favella, 2014; Kiverstein & Miller, 2014), dynamical systems theories (Beer, 1995; van Gelder, 1998), theories about engagement with the world and the sensorimotor approach to perception (Buhrmann et al., 2013; Di Paolo et al., 2014; Di Paolo et al., 2017), and even the older branch of ecological psychology (Gibson, 1966, 1977, 1979). Such approaches all stress the emerging idea of the embodied mind, by which the human mind is fundamentally constituted by the dynamical interactions of brain, body and environment (Tikka & Kaipainen, 2014). Crucial in this new approach is the role of actions and interactions in the construction of knowledge, which make it arguable to conceive of an "enactive turn" in the sciences of mind, as a further extension of the embodied approach to cognition.

Embodiment and the enactive approach

The "embodied approach" to cognition has seen two major strands. First, there has been the *experientialist approach* of cognitive semantics that attempts to characterize meaning in terms of the nature and experience of the organisms doing the cognizing. It describes meaning in terms of embodiment, which should be considered as our collective biological capacities as well as our physical and social experiences as beings that function in an environment. The basic epistemological finding of this approach was that knowledge must be understood in terms of structures of embodied human understanding and as the result of the interaction of an organism with its environment (Lakoff, 1987, 1988; Lakoff & Johnson, 1980, 1999; Johnson, 1987, 2007, and Reybrouck, 2001a, 2005 for musical applications). This approach, though seminal, has faded somewhat into the background in recent contributions about embodied cognition. The other strand is the *sensorimotor approach*, which has generated a lot of interest and debate in the cognitive science community over the last decades. Being more firmly grounded in experimental and empirical research, it brings together insights from fields so divergent as active perception, dynamical systems theory, ecological psychology, phenomenology, cybernetics and neuroscience (Buhrmann et al., 2013). Its main argument is that both the content and form of perceptual experience are constituted by ongoing knowledge of sensorimotor regularities and contingencies, rather than relying on computations in the brain. Perceivers, in this view, are "active agents" who engage with the world, which means also that perception is linked to skilful action (O'Regan & Noë, 2001).

The "enactive approach" is closely related to the embodied and sensorimotor approach (see Reybrouck, 2021, for a broad overview). It was introduced in cognitive science to unify several related ideas (Varela et al., 1991) and has been summarized by Thompson (2007) in five major claims: (i) living beings are autonomous agents that actively generate and maintain themselves by actively generating and maintaining their cognitive domains; (ii) the nervous system is an autonomous dynamic system that actively generates and maintains its own coherent and meaningful patterns of activity to create meaning; (iii) cognition is the exercise of skilful know-how in situated and embodied action with cognitive structures and processes emerging from recurrent sensorimotor patterns of perception and action; (iv) the world of a cognitive being is not a prespecified, external realm, represented internally by its brain, but a relational domain that is enacted or brought forth by that being's autonomous agency and mode of coupling with the environment; (v) experience is central to any understanding of the mind and needs to be investigated in a careful phenomenological manner. As such, mind science and phenomenological investigations of human experience should be pursued in a complementary and mutually informing way (Thompson, 2007, p. 14). As a new emerging field, however, the enactive approach still has to come to age. There are, as yet, a lot of conflicting and competing theories or doctrines with distinct labels, such as enactive cognition, enactivism, enactive cognitive science, sensorimotor enactivism, weak enactivism, radical embodiment, (radical) embodied cognitive science, conservative enactive or embodied cognition, embodied mind, embodied dynamicism and others (Chemero, 2009; Colombetti, 2007, 2014; Froese et al., 2013; Gibbs, 2010; Gallagher & Zahavi, 2008; Hutto & Myin, 2013, Maiese, 2011; Noë, 2004; Shapiro, 2014; Silverman, 2013, and Thompson, 2007 for an overview).

Enactivism, in its current form, is still a complex tapestry of interrelated and mutually supporting ideas from fields as disparate as cognitive science, biology and the philosophical tradition of phenomenology. It incorporates new empirical studies as well as theoretical perspectives and traces its sources from phenomenological philosophies (Husserl, Merleau-Ponty), pragmatism (James and Dewey), Gestalt psychology, the cybernetics of the 1940s and 1950s, and ecological psychology (Di Paolo et al., 2010). Central in the enactive approach, however, is a conceptualization of sense-making by organizing the ongoing stream of experience. Enactive frameworks, then, stress the role of embodied action and active exploration, which means that consciousness is not brain-bound but something that extends beyond the skin and skull. In other words: the mind does not stop where the rest of the world begins, and what is outside of the body is not outside of the mind (Clark & Chalmers, 1998). This “extended cognition” or “extended mind” approach is currently the object of heated discussions in the context of the philosophy of mind, and has found a more or less safe haven in the new field of *4E cognition*, which is an umbrella term for the terms Embodied, Embedded, Extended and Enacted. Cognition, in this view, involves the entire body of a living system (embodied); it is co-determined by physical, social and cultural aspects (embedded); it is offloaded into biological beings and nonbiological devices, such as, e.g., a notebook, a computer or a smartphone (extended); and it implies a mutual exchange between a living organism and its environment (enacted) (Menary, 2010; Newen et al., 2018, and Schiavio & van der Schyff, 2018 for musical applications).

Cognition, on this view, is not encapsulated in the brain but calls forth interactions with the environment. Such interactions can be manifest, as in the case of playing a musical instrument, with actual physical actions being performed on sound-producing devices, or virtual as in the case of epistemic interactions that deal with music at the level of imagery or symbolic computations. Both kinds of interactions, however, are not strictly opposed to each other, but show continuous transitions, as advocated already by the Kharkov school in Russian psychology in the 1930s, central in which approach was the role attributed to actions in the “formation of mental acts” with an assumed transition from overt actions to mental actions at an internalized level of performing (Gal’perin, 1992; and Haenen, 2001 for an overview).

The claims are related to the *motor theories of perception* with a dynamic tension between sensorimotor processing and ideomotor simulation (see Reybrouck, 2001b for an overview). The “sensorimotor” aspect is conservative in the sense that it deals unceasingly with sensory input being linked to the central nervous system and the effector organs. It means that an observer is in continuous interaction with the environment in an attempt to minimize the deviations and to keep the disturbances without critical limits (Berthoz, 1996, 1997; Paillard, 1990, 1994). The “ideomotor” approach, on the contrary, takes more distance to the actual sensory input and allows perceivers to simulate the actual unfolding of the stimuli and their possible relationships at a virtual level of imagery (Prinz & Chater, 2005). Both approaches, further, are not opposed but may complement each other. Applied to music, this means that music processing affects both our executive (the muscles) and our sensory system (the senses) as well as our mental simulations. As such, listening is to be considered as an adaptive process of sense-making that is externally oriented and that keeps pace with the sonorous unfolding. Music cognition, then, is not restricted to the brain (internalist approach), but extends beyond the brain to encompass our whole body and its interactions with the environmental sounding world (externalist approach). It implies a richer and more holistic model of music cognition that revolves around the concept of embodiment and the phenomenological experience of music and argues for an engagement with music in the course of a lived experience (Reybrouck, 2017b, 2019; Schiavio et al., 2017a, 2017b).

Neuroscience and the mapping of the musical experience: Neurodynamics and neurophenomenology

It can be questioned to what extent there is a mapping between the sonorous unfolding of the music and the processing by the listener in real time. We may wonder also to what extent listeners are aware of such possible mapping. There are two main approaches to tackle this problem: *objective measurements* and *subjective appraisals*, somewhat related to the distinction between "third-person" and "first-person" descriptions of consciousness (see Varela & Shear, 2002). The objective measurements can be reduced mainly to behavioural and brain-based measurements, which aim at tracking the graded nature of consciousness, and which distinguish between unconscious and conscious processing (Seth et al., 2008; Dulany, 1997). Behavioural measurements, first, claim that a mental state can express its content in behaviour—such as, e.g., choice behaviour, deliberate use of knowledge according to instructions, introspective reports, confidence ratings to test awareness of knowing and post-decision wagering regarding the outcome of a discrimination— and that such expressed contents are conscious. Brain measures, on the other hand, should enable us to obtain objective measurements of what is going on in our brain. Several distinct techniques can be envisioned here, such as EEG, MEG, event-related potentials (ERPs), widespread activations patterns, measurements of neuronal synchrony and connectivity, but the most challenging new developments in this field are those which are related to continuous and ongoing measurements of psychophysiological responses.

An important contribution in this regard is the *neurodynamic approach*, which refers to those neurocognitive theories that highlight the role of transient large-scale patterns of rhythmically coordinated neural activity that spans multiple regions of the brain (Freeman, 1997; Bressler & Kelso, 2001, 2016; Varela et al., 2001; Cosmelli et al., 2007; Sporns, 2011, and Barrett & Schulkin, 2017 for an overview). This coordinated neural activity provides the ability to register responses that differ not only in kind but also in granularity, complexity and differentiation (Lindquist & Barrett, 2008), as contrasted to traditional approaches that focus merely on functional specialization and localization as commonly adopted by computational theories of neural functioning. Broadly speaking, the neurodynamic approach diverges from stable processing pathways by claiming the multifunctionality of neural structures at multiple scales (Anderson, 2014; Anderson et al., 2013).

The neurodynamic approach has been applied already to the field of music cognition (Large, 2010; Flaig & Large, 2014) with ground-breaking research into the relationship between bodily movement and music and the sensorimotor involvement in music perception (Chen et al., 2008; Large et al., 2015). The most challenging part, in these studies, is the empirical verification of the findings, as there is need for high temporal resolution data that show how relevant characteristics of neural dynamics change during musical experience and how these measures correspond to differences of experiential granularity and complexity (Garrett et al., 2013; Barrett & Schulkin, 2017). Much is to be expected here from high temporal resolution techniques such as EEG and MEG which can measure the moment-to-moment brain signal variability that is associated with cognitive functioning.

Besides these objective measurements—labelled also as third-person descriptions—, there are subjective appraisals or first-person descriptions. There is, in this regard, the new emergent field of *neurophenomenology* (Varela, 1996; Lutz, 2002; Lutz & Thompson, 2003; Thompson, 2004), which enriches the theoretical perspective of phenomenology with the tools of neuroscience and experimental psychology. It is an approach that stresses the usefulness of obtaining detailed, first-person reports of the moment-to-moment subjective experience of what we perceive, showing up with varying degrees of significance and relevance, and depending on our current states of expectation, attention, motivation and emotion (Fazelpour & Thompson, 2015). This neurophenomenological approach is challenging and promising, but it is still in the early stages of development. It is hoped, therefore, that the program should be able to predict phenomenal states based on physiological states, but there are still major conceptual and methodological difficulties which are related to this approach, both in establishing the correlations between the identification of certain internal functional states and the phenomenal states (Cleeremans & Haynes, 1999). Yet, the promotion of relationships between phenomenology and experimental neuroscience may extend both domains and may lead to a productive co-determination in the sense that progress in neurosciences could motivate a more finely detailed phenomenological description and a more detailed phenomenology could contribute to a better definition of an empirical research program (Le Van Quyen, 2003, 2010).

Neuroscience and the aesthetic experience of music: Neuroaesthetics

How can the above be linked to the processing of music? There is, as yet, a new domain that is known as *neuroaesthetics* (Chatterjee, 2010; Leder, 2013; Nadal & Skov, 2013; Pearce et al., 2016; Chatterjee & Vartanian, 2016; Zaidel et al., 2013; Zeki, 1999, 2013), and in a more restricted sense, the neuroaesthetics of music (Brattico, 2015; Brattico & Pearce, 2013; Brattico et al., 2009-2010; Brattico et al., 2013; Brattico et al., 2017). Starting from the seminal work of Zeki, who first coined the term (Zeki, 1999), neuroaesthetics can be understood as the inquiry into the neurobiological substrates of the aesthetic experience. Its principal goal is the empirical study of those brain mechanisms which are involved in the appreciation of art and aesthetics. Due to the development of new neuroscientific methods, it has emerged as a proper new research field that is not merely interested in providing a catalogue of brain regions that are involved in aesthetic or artistic activities, but at uncovering also the underlying mechanisms. Its focus, therefore, is not limited to particular classes of objects but should concern the particular way how objects can be experienced when approached with an aesthetic attitude (Cupchik, 1992; Nadal & Skov, 2013). As such, it is concerned with the perception, production and responses to works of art or objects of aesthetic value. There may be a problem, however, as to the rather gratuitous way of defining concepts as “works of art”, “aesthetic value” and “aesthetic experience”. To contribute in a meaningful way, they should be generalizable to account for varieties across art and aesthetics across many human cultures. Art, moreover, is not the only source of aesthetic reactions (Brown & Dissanayake, 2009; Dissanayake, 1992), as aesthetic concerns permeate a broader range of activities and objects which are related to the communication and experience of spiritual, ethical and social meaning. There are, as such, numerous sources of aesthetic experiences, such as nature scenery, food, music, human faces, smells and many others, implying a biological ancestral origin for these reactions.

Neuroaesthetics, then, should try to explain the evolutionary basis of the neural mechanisms that endow humans to produce visual, auditory, olfactory, gustatory, tactile and kinaesthetic experiences (Zaidel, 2009; Zaidel et al., 2013) and to engage in rewarding sensations in different modalities. An understanding of the underlying mechanisms, however, is still elusive to some extent (Brattico et al., 2009-2010).

It can be argued, in this regard, that there is something common in the sources that arouse aesthetic emotions when they are experienced as being aesthetically beautiful, with neural correlates in a part of the emotional brain that seems to be involved in the experience of beauty. Experiments aimed at determining which activity in the brain correlates with that experience have repeatedly shown one specific locus in the brain, namely the medial orbito-frontal cortex (mOFC) (Ishizu & Zeki, 2011, 2014; Zeki, 2014). Such activity has been found regardless of whether the source was visual, musical or mathematical, and, more importantly, the activity in the mOFC is detectable and quantifiable in an objective way. This holds true, even though such experience is subjective as it relates to private experiences in individual brains. These early findings precipitated further neuroimaging studies, revealing activity in the reward circuit as a whole to be a key component of aesthetic experience. Positive feeling of liking or enjoying beauty are the product of an interplay of processes that are related to reward value representation, prediction and anticipation, affective self-monitoring, emotions, and the generation of pleasure that take place in cortical and subcortical regions, as well as some of the regulators of this circuit (see Nadal & Skov, 2013 for an overview).

One can ask, to what extent the experience of beauty, or aesthetic reactions in general, should be considered in terms of generic survival strategies or as domain-specific reactions to a rather constrained subset of our environment? Humans are unique biological organisms that display an aesthetic orientation towards rewarding stimuli, but the involved brain regions seem to be involved also in other kinds of experience, which could suggest that aesthetic experiences rely on neural mechanisms that are nonspecific and general—such as attention- and motivation-related processes—, which we share also with some of our close primate relatives (Zaidel et al., 2013). Aesthetic experiences, in this view, seem to rely on the interaction between domain-general neural processes such as those involved in attention, motivation and reward, and artwork-derived sensory processes.

All this holds for aesthetic experiences in general, but the findings can be generalized also to music. Evaluative and contextual conditioning aside, aesthetic appreciation appears to be a dominant value of human musical experience (Juslin & Laukka, 2004). Certainly, abundant evidence from research with so-called “WEIRD” populations—i.e. the thin slice of humanity that comprises Western Educated, Industrialized, Rich, and Democratic societies (Henrich et al., 2010)—confirms that—in the case of a favourable environment and listening situation—listening to or performing music effectively generates aesthetic experiences that may include specific emotions and evaluative judgments of beauty, aesthetic quality and liking. Such an aesthetic experience has been defined by Brattico & Pearce in operational terms:

> [w]e define an aesthetic experience of music as one in which the individual immerses herself in the music, dedicating her attention to perceptual, cognitive, and affective interpretation based on the formal properties of the perceptual experience. (Brattico & Pearce, 2013, p. 49)

There seem to be three major outcomes of such an experience, namely emotion recognition and induction, aesthetic judgment, and liking and preference, which typically combine to form a genuine aesthetic situation. It is thus necessary to consider not only the properties of the music but also the listener and the listening situation as constituting parts of an aesthetic experience. The most prevailing question, however, is how we can measure and assess the essence of such an aesthetic experience. The answer probably is to be found in the combination of implicit measurements such as physiological responses spread out over the whole body and neural activity located in the brain. As to the latter, a chronometric model of the aesthetic musical experience has been proposed by Brattico and colleagues which embraces successive processing components, such as feature analysis and integration, early emotional reactions, cognitive processing of rules and stylistic standards, the experience of discrete emotions, the experience of aesthetic judgments and aesthetic emotions (not mandatory), and conscious liking of the music. Each of these processing stages has a specific place in the time scale of the aesthetic experience and specific brain structures can be linked to them (Brattico et al., 2013).

Listening as adaptive behaviour: Neuroplasticity

A musical-aesthetic experience is not merely a kind of passive listening but entails an active engagement with the sounds. This is obvious in performing or playing a musical instrument, but it holds also for active listening. The question in this regard is whether there are lasting effects at the neural level of prolonged listening, or put differently: Can listening be considered as adaptive behaviour with plastic changes in the brain a possible outcome? There is already abundant literature on music and the plastic brain (see Reybrouck et al., 2018b for an overview) and musical expertise has become a useful model for investigating practice-related brain plasticity in humans (Dawson, 2011; Fauvel et al., 2014). Most of this research has focused on performing rather than on listening, yet it has been found recently that music listening and playing overlap to some extent, as there is an (en)active component in listening and an auditive-perceptual component in performing (Reybrouck, 2001a, 2001b).

A distinction should be made, however, between musical laymen without any practice-related experience, and those listeners who have a history of active musicianship. The latter can engage with music at a virtual level of motor or embodied simulation (Gallese, 2005), but even those without musical training have shown activity in some motor areas of the brain. It is somewhat premature, however, to draw definite conclusions at this moment as abundant empirical findings are still somewhat lacking. Much depends here on the actual modalities of presentation of the sounding stimuli, which can embrace only the auditive modality—as in merely listening without seeing the performers—or a combination of sensory modalities—such as the auditive, the visual, the tactile and the kinaesthetic one. The resulting sensory experience can result either in perceptual immediacy or in a more detached experience, with differences in *gradation of witnessing*, as the kind of first-hand experience of a living experience that represents reality with the fullness and richness of the actual time and place of a particular performance (see Reybrouck, 2016, 2017c for an overview). Besides the level of witnessing, there is also the phenomenon of *sensorial effectiveness*, which means that animals (and man) mostly use more than the traditional five senses to communicate with each other (Sebeok, 1990). It is a conception which is closely related to the concept of "multisensory integration" (Stein et al., 2014; Russo, 2019), which means that there is an increase in neuronal response to a stimulus that consists of a combination of sensory modalities as compared to the responses to each modality in isolation (Pantev et al., 2009). It can be argued that this holds even more when the multisensorial character of the stimuli is expanded with motor elements, as in sensorimotor integration or sensorimotor contingencies (O'Regan & Noë, 2001).

Listening to music, moreover, relies upon multiple listening strategies, which means that the responses that are the outcome of them are no linear function of the music. There are definitely innate biological predispositions that determine some primary reactions to the music—e.g. startle reflex after sudden loud sounds, reactive behaviour, and some primordial emotions—as well as learned and acquired reactions which are the outcome of an individual learning history. As such, there is a complementarity of phylogenetic disposition and ontogenetic development with a dynamic tension between nature and nurture. The learning history, in particular, is quite interesting for the enactive and embodied approach. It highlights the role of interactions with the sounds and the resulting activation of neural circuits, which may even lead to plastic changes in the brain. The brain, in fact, is a complex system that dynamically adapts to continuously changing environments over multiple time scales and that can be physically changed by both internal and external factors (Bassett et al., 2011). This holds also for physical interactions with sound-producing devices as in learning to play a musical instrument.

As such, there has been a bulk of contributions that have studied the adaptive changes that are the outcome of active engagement with music and musical instruments and which can be subsumed under the umbrella term of *neuroplasticity* (see Reybrouck & Brattico, 2015, Reybrouck et al., 2018c for an overview). These contributions encompass the processes by which the brain is remodelled to some extent and include the formation of new neurons and glial cells (neurogenesis), the formation of new connections, and modifications of existing ones through multiple processes such as the formation and elimination of synapses (synaptogenesis and synaptic atrophy), dendritic remodelling, axonal sprouting and reduction of synaptic connections or pruning. An important factor in this remodelling is the level of activity or demand, especially at a young age but also in the adult brain some remodelling is possible, with reported measurements of birth, migration, maturation and functional integration of new neurons in the brain (Kays et al., 2012).

The study of music-related neuroplasticity, further, has seen two major strands of research, namely "morphometric" and "functional" studies. These studies are well-documented and have shown neuroanatomical and neurophysiological adaptations, which can be reduced to the rapid unmasking of existing connections and the establishment of new ones. These plastic changes can be demonstrated at two levels, namely the gross anatomical differences between professional musicians and laymen (macrostructural) and the subtler functional differences after enhanced and prolonged musical practice or experience with finer modifications of synaptic strength in distributed cortical networks (microstructural). Evidence from primarily WEIRD research demonstrates that the brains of individuals with musical training, in particular, show differences in volume, morphology, density, connectivity and functional activity across a broad range of brain regions and structures, with as underlying hypothesis that functional reorganization may cause structural adaptation (Bangert et al., 2006; Münte et al., 2002, Fauvel et al., 2014, Merrett et al., 2013). At the macrostructural level, differences between musically-trained and musically non-trained participants include the size of the primary motor cortex, the cerebellum, the planum temporale, Heschl's gyrus, but also in white-matter tracts such as the corpus callosum, the corticospinal tract and the arcuate fasciculus (Bengtsson et al., 2005; Imfeld et al., 2009; Moore et al., 2014; Öztürk et al., 2002); at the microstructural level adaptations can be shown at the level of individual neurons and synapses to change the neural effectivity.

These structural changes indicate only one part of the story. Besides these, there are also functional adaptations, which mark to some extent the distinctive ways of dealing with music that set trained performers apart from their contemporaries. The experience of instrumental performance does not only refer to an embodied process of sound production; it appears also to shape the individuals' experience of listening, in the sense that trained musicians can imaginatively re-enact the sound-producing physical acts whilst listening. Several empirical studies have shown that music listening may enhance motor facilitation, allowing listeners—within the limitations of their motor repertoire—to re-enact the same motor actions that are required to perform the music that is heard (see Gordon et al, 2018 for an overview). Listeners, then, may perceive music through motor engagement (Schiavio et al., 2017a). These findings are still scant and tentative to some extent, though they have gained momentum in the newly emerging field of 4E cognition. The embodied approach, moreover, with its emphasis on sensorimotor interactions, seems to be a welcome addition to the more cognitive detached approaches to music listening that have been prevailing in former decades (see Reybrouck & Brattico, 2015 for an overview). For example, proprioceptive awareness is highly relevant during musical practice. Evidence from research with highly trained classical musician participants (e.g. Altenmüller, 2008) indicates that prolonged musical experiences may lead to different tactile sensitivities compared to other populations (Zamorano et al., 2015).— Findings from embodied music cognition research, then, suggests that prolonged musical experiences – either active during performing or passive during listening—might influence the nature of musicians' "performative awareness" of the body (Acitores, 2011; Gallagher 2005, p. 220), possibly influencing the way in which trained musicians recognize feelings, movements, thoughts and beliefs to be their own.

Neural connectivity and the networks of the brain: Connectomics

Active engagement with music can be described in terms of "adaptive behaviour." At the perceptual level, this correlates with the ability to identity and process acoustic variations in the acoustic environment. This ability, which is grounded in our biological predispositions, can be refined as the outcome of a learning history with plastic and adaptive changes at the structural and functional level of the functioning of the brain. Experience-driven neural activity can shape the refinement of our neural circuitry with modifications in synaptic connectivity. It acts as a basis for facilitating learning and memory through modification of the neural circuits with an increase in synaptic strength, which may be persistent and which may even be recorded during rest (Chaudhury et al., 2008; Damoiseaux et al., 2006; Martin & Morris, 2002).

The majority of earlier studies has focused on the study of independent activity in separate brain structures. Though interesting, this approach to the neural correlates of brain function was limited to some extent. The past decade, therefore, has seen a shift from *brain localization studies* to the study of the interactive communication between brain structures. This is the emerging field of *connectomics*, which exploits algorithms and concepts which were developed within the field of network science, and which has as a final goal to generate a complete map of all neural connections by describing the brain as a large structural network that is made of neural connections, consisting mainly of white matter tracts and grey matter (Moore et al., 2014). Such network characterization rests on several motivations: it comprises networks of brain regions that are connected by anatomical tracts and/or by functional associations; it can reliably quantify these networks with a small number of measures; it can explore structural-functional connectivity relationships by defining both structural and functional connections on the same brain regions; and it can reveal presumed network anomalies or neurological and psychiatric disorders (see Rubinov & Sporns, 2010, for an overview).

Network science, as applied to the neurosciences, provides techniques and analysis methods. It allows in vivo examination of anatomical and functional interactions on a whole-brain scale to obtain information of the amount and direction that activity patterns in particular brain regions exert over one another (Fauvel et al., 2014). Several techniques are currently available such as diffusion tensor imaging (DTI, MRI), fibre tractography, stochastic dynamical modelling and whole-brain computational modelling (Cabral et al., 2014). Tractography is very suitable for examining the anatomical connectivity between distinct brain regions by highlighting how white matter fibres connect each brain region; fMRI and MEG, on the other hand, provide useful information for functional connectivity in terms of temporal interdependence of neuronal activity patterns in anatomically separated and removed brain regions and the communication between them, to be measured by the level of simultaneous coactivation of fMRI and MEG time-series in these regions. Such methods make it possible to study the brain as an integrated network and to gain insights about large-scale neuronal communication in the human brain (van den Heuvel & Hulshoff, 2010).

This integrated network, moreover, consists of multiple sub-networks, which can be considered as distinct connectivity networks. The findings are still somewhat elusive up to now, but two alternating network systems, which have been coined as "task positive" or "task negative" networks have been identified already. The former, coined as "looking out" or "executive function systems," are recruited in case of active engagement and goal-directed tasks with focal attention and evaluation of the salience of external stimuli; the latter, called "resting networks," are related to the spontaneous oscillations (low-frequency BOLD fluctuations) of the resting brain (Buckner et al., 2008; Fox & Greicius, 2010; Raichle, 2015; Raichle & Snyder, 2007). Such correlations between distinct areas of the brain point into the direction of organizational networks, which can be studied by measuring the synchronization of their spontaneous fMRI oscillations at rest and which make them indicative of the level of cognitive functioning in general. There seems to be, in fact, a link between the organization of the brain network and task performance, such that the functional connectivity patterns may be used as a predictor for cognitive performance.

Most interesting from the point of view of enactive and embodied cognition, is the finding that the resting-state connectivity is not an established and fixed property. It is a state that can be modulated and shaped by recent experiences and learning histories, both within and between the networks that are recruited, suggesting a consolidation of resting-state brain activity as the result of learning (Fauvel et al., 2014). The brain, in sum, consolidates recent learning and maintains the association of activity of brain areas that are likely to be used together in future (Fox & Raichle, 2007). As such, 10 to 12 *resting-state networks* have been identified in the cerebral cortex, such as the motor cortex network, the visual and auditory networks, the default mode network and attention and memory-related networks, which all represent some intrinsic form of brain connectivity with temporal correlations between spatially discrete regions (Luo et al., 2012). In contrast to task-related networks, these resting-state networks observe the brain in the absence of overt task performance or stimulation and are used for the identification of correlations or "functional connectivity" between remote brain areas (Friston et al., 1993; Horwitz, 2003; Rogers et al., 2007)

One of these networks, the *default mode network* (DMN)—a network located in the medial orbitofrontal, anterior and posterior cingulate cortex—, is of particular interest. It can be understood in two ways, either as related to intrinsic "activation," as in particular ways of cognitive functioning, or as a kind of "deactivation" during other goal-directed tasks (Buckner et al., 2008; Gusnard et al., 2001). It has been related to specific functions such as self-referential thoughts, emotional perspectives, levels of self-estimation and self-awareness and cognitive appraisal. This network seems implicated in the constant monitoring of our sensory environment; most interestingly, it displays high activity during lack of focused attention on external events (Fox & Greicius, 2010; Immordino-Yang et al., 2012; Raichle, 2015). Generalizing a little, it seems to function as a toggle switch between outwardly focused mind states and the internal or subjective sense of self (Wilkins et al., 2014).

It is tempting to apply this to the realm of music—and the study of brain connectivity is indeed on the current agenda within the neurosciences of music. Better understanding of resting-state networks has the potential to inform what is known about how our brains respond to music, both in cognitive, emotional-affective and sensorimotor terms. It has been found, moreover, that musical training might enhance an increased resting-state connectivity by triggering heightened connections between brain regions that are structurally and functionally altered as the result of music training. Most important, in this regard, are the manifestations of this connectivity during rest and during task-free conditions, which has been coined also as the "silent" imprint of musical training on the human brain (Klein et al., 2016). This research is still in its infancy but increased connectivity for musicians has been found between seed regions for which plastic changes was shown already in musicians, such as the prefrontal, temporal, inferior-parietal and premotor areas. The findings point into the direction of four networks that supply integrative interpretations for cognitive functions during musical practice: (i) autobiographical memory-related regions belonging to the default mode network (triggered by the encoding, storage and recall of melodies with an emotional and biographical quality); (ii) areas belonging to the salience network with access to semantic memory (music stored in terms of verbal labels and auditory structure); (iii) regions implied in language processing and the resting-state auditory network, and (iv) structures belonging to the executive control network (sub-serving the motor modulation required for an emotionally expressive interpretation of music) (Fauvel et al., 2014). This network organization can change smoothly over time and is modulated by exogenous stimulations as well as by spontaneous activity during rest. As such, it has been hypothesized also that the obtained connectivity patterns are the result of music-related mentation, outside of the context of actual performance, and that they can dynamically change during music listening (Bassett et al., 2011; Cabral et al., 2017; Klein et al., 2016).

The findings, though still somewhat tentative, are challenging. They highlight that music, as a cognitive-demanding activity, may stimulate neuroplasticity and neurodevelopmental improvement by recruiting multiple forms of working memory, attention, semantic processing, target detection and motor function, which all serve general functions rather than music-specific regions of the brain (Janata et al., 2002; Karmonik et al., 2016). This holds for active music playing but also for attentive music listening, which engages the co-activation of many processes that involve widely distributed and partly interchangeable substrates of the brain (Cuddy & Dufin, 2005). The picture that is emerging is that attentive music listening is associated with neural connectivity patterns rather than a one-to-one mapping to single brain structures (Sachs et al., 2016).

The study of brain connectivity during music listening is thus an emergent field. Three major strands of research crystallize: (i) ongoing task-related connections while listening to or making music, (ii) resting-state connections, which are active before or after musical activity, and (iii) the relations between task-related and resting states. The study of task-related connections is quite obvious, relating neatly to programs of enquiry within enactive and embodied fields of music cognition research, and in step with the study of sensorimotor coordination or contingencies. The role of the default mode network (DMN), on the other hand, is gaining momentum as well. It is one of the most discussed brain circuits in current neuroimaging studies, but studies on the DMN as related to music listening are still rather rare. Some findings have shown a relation between the DMN and intense aesthetic experiences (Vessel et al., 2012; Vessel et al., 2013) and aesthetic music listening—in particular while listening to preferred music— with differences in brain connectivity between auditory brain areas and the hippocampus, which point into the direction of a coupling with the hedonic networks (Wilkins et al., 2014; Koelsch & Skouras, 2014). Listening to sad music, in particular, seems to be associated with higher centrality of the default mode network hubs, fewer connections with other brain regions and more induced mind-wandering (Taruffi et al., 2017; Alluri et al., 2017).

The findings are promising. Bringing together contributions from neuroimaging, network science and connectomics, they seem to provide the needed framework for studying the role of the human brain while dealing with music. Some findings deserve special attention, such as the involvement of the medial structures of the brain which are related to the default mode network (in particular while listening to our favourite music), the convergence between aesthetic responses and the connectivity of the reward circuit with the inferotemporal cortex, and the connectivity of the audiomotor networks with the default mode network (see Reybrouck et al., 2018a for an overview). As such, it is possible to collect the much-needed neurological underpinnings of the neuroaesthetics of music and of the aesthetic experience of music, which revolves mainly around the neurobiological approach to music, thereby integrating perceptual, cognitive, and affective levels of processing, soliciting the reward circuit, the DMN, and engaging the connectivity of the brain as a whole. Functional connectivity between brain networks related to aesthetic judgment, evaluative or even moral decision making, and the reward brain system has been demonstrated empirically (Avram et al., 2013; Karmonik et al., 2016; Kringelbach & Berridge, 2009; Sachs et al., 2016; Salimpoor et al., 2013). Yet the link between the functioning of the DMN and music processing is still a subject of debate, both during the task-related process of actual listening and during resting states. It is currently hypothesized that the functional connectivity observed during music listening could be linked to the beneficial impact of musical aesthetic experiences (Alluri et al., 2017)

Conclusion and perspectives

The relation between cognitive neuroscience and the embodied approach to cognition has been problematic up to now, due to the prevailing opinion that neurosciences are mainly concerned with encapsulated static structures within the brain. Even the development of recent measurement techniques in the domain of connectomics has focused to some extent on static representations of connectivity patterns. Yet there is both scientific intuition ad recent empirical evidence that connectivity can be modulated both spontaneously and as the result of exogenous stimulation. The brain is a complex system with many interacting parts that dynamically adapt to a continually changing environment over multiple time scales. On the short temporal scale, rapid adaptations and continuous evolutions of these interactions and connections form the neurophysiological basis for behavioural adaptation or learning, both at the level of individual synapses between neurons and at the level of regional changes in brain activity and connectivity between distinct regions (Bassett et al., 2011). As such, there has been a transition from a search for anatomical markers of sensorimotor, cognitive and affective-emotional functioning to the finding that our brain is fundamentally plastic and adaptive, both on the short-term and long-term. Central in this new emerging paradigm is a conception in terms of *brain dynamics*, revolving around the exploration of a temporally evolving network architecture of the brain as the outcome of neurophysiological adaptability that facilitate the participation of cortical regions in multiple functional communities.

This is evidenced by structural changes of the tissues of the brain (neuronal masses and white fibres) but also by modifications of the brain circuitries as the outcome of early and whole life span experiences. It is here that the relation with the *embodied/enactive approach* to music cognition becomes most visible. The functional connectivity of the brain, in fact, is not fixed but is based on a dynamic community structure, which is modifiable by recent experiences and learning histories. As such, it is possible to relate it with the networks of the brain, which are modulated both by exogenous stimuli and spontaneous activity during rest. Given the abundance of sensorimotor coordinations and ideomotor simulations that are prompted by active engagement with music, it seems likely that music can trigger modifications between and within these networks. The question to what extent the functional connectivity in the brain differs as a function of musical expertise during continuous music listening in naturalistic conditions, however, still needs further investigation. In a ground-breaking recent study, Alluri and colleagues found a difference in connectivity between musically-trained and non-trained participants in networks engaged in music perception and action, with trained musicians showing more enhanced connectivity of sensorimotor regions in the brain, where those without training relied more narrowly on left hemispheric auditory regions (Alluri et al., 2017). Using full-brain connectivity analysis, the authors reported that trained musicians displayed higher connectivity in action-related networks. Experienced performers thus displayed better integration of motor and sensorimotor regions during passive music listening, with, in particular, enhanced connectivity with the motor and sensory representation of the upper limb and torso. Such findings provide further support for the idea that musical expertise strengthens the brain mechanism that link *action and perception*.

This brings us to some clinical and educational claims. It has been found that formal instruction in music at an early age may lead to more profuse and efficient connections in the brain, even in the case of apparently passive music listening. Musical performance training in particular has also been seen to increase the coherence patterns of the connections within the brain (Flohr & Hodges, 2002; Flohr et al., 2000), suggesting diagnostic and developmental implications of further research in this area. A major finding in this regard is the discovery of expertise-modulated hubs which surface in the networks of the brain of trained musicians during music listening, with key hubs in the cerebral sensorimotor regions. This contrasts with dominant hubs in the parietal and left-hemispheric temporal regions for those without specific music training, suggesting differences in listening strategies between the two groups. Musicians who start training at an early age may also exhibit greater centrality in the auditory cortex and those areas that are related to top-down processes, attention, emotion, somatosensory processing and non-verbal processing of speech (Alluri et al., 2017, p. 12). Such modifications of the brain networks may have consequences for diagnostic purposes and developmental interventions across all childhood populations.

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Biography

Mark Reybrouck studied physical education, physical therapy and musicology. He is actually emeritus professor at the University of Leuven and guest professor at Ghent University. His interests are interdisciplinary in their claims with an attempt to bring together insights from the fields of psychology, biology, semiotics and music. His actual research agenda concerns musical sense-making with a major focus on musical semantics and biosemiotics as applied to music and music and brain studies. At a theoretical level he is involved in foundational work on music cognition and perception, especially the biological roots of musical epistemology and the embodied and enactive approach to dealing with music. Besides this theoretical work, he has been involved in empirical research on representational and metarepresentational strategies in music-listening tasks. He published a lot of papers in internationally reviewed scientific journals and book chapters. He is also author and editor of several books about listening strategies and cognitive strategies for dealing with music as well as edited volumes on musical semiotics and music and brain studies. His most recent contributions cover the field of embodied and enactive cognition and the domains of neuroaesthetics and neuroplasticity as applied to music.