Neurons Behind Notes: An Interdisciplinary Exploration Bridging Psychology and Neuroscientific Insights for Music Learning, Performance, and Pedagogy

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Abstract

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The purpose of this paper is to review and analyze the literature in educational neuroscience as well as music cognition, exploring new insights in psychology and neuroscience concerning learning and brain plasticity in the last thirty years. This serves as an interdisciplinary study and manual for musicians, providing fundamental scientific concepts that potentially answer “why” and “how” music is perceived and performed. Analysis of these fundamental concepts provides a basis for greater understanding of performance and pedagogical approaches to learning and teaching music. This will include an overview of educational neuroscience and music cognition, the fundamentals of neuron structure and function in learning and memory, a large literature review of studies concerning musical training and its effects on plasticity, a proposal for preliminary experiments on hippocampal cell firing in relation to accuracy and memory, as well as important literature concerning long-term memory functions, motor skill acquisition, and creativity.

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Introduction

Research Question:

How do interdisciplinary approaches, bridging insights from psychology and neuroscientific research, contribute to a holistic understanding of music learning, performance, and pedagogy, particularly focusing on the neural mechanisms behind these processes?

This research paper aims to investigate the synergies between psychological and neuroscientific perspectives in the context of music, with a focus on how these insights can inform our understanding of music cognition and education.

Background and Current State of Research:

One of the most complex organs in the human body, the brain contains vast networks of neurons that facilitate the execution of simple tasks to solving challenging problems which require higher cognitive loads. Through the evolution of brain structure and function, one of the most natural elements that distinguishes us as human beings is the ability to perceive and make music (Trimble & Hesdorffer, 2017). Furthermore, the perception and production of music is one of the most complex human skills, utilizing most brain regions (Altenmüller, 2022). It is an incredibly rich cognitive, sensory-motor, visual, and emotional human experience. Listening to and making music are extremely involved tasks, involving sound perception, movement, coordination, expectation, planning, and error-correction, alongside strong emotional components. The physical as well as emotional sides of music performance involve a large network of cortical regions as well as subcortical areas. The faculties involved operate as an interconnected network dynamically adjusting to external stimuli. This demonstrates the significance of investigating brain plasticity within the context of music education, training, and proficiency, as it reflects the brain's remarkable capacity to conform to varying environmental demands. This paper provides current knowledge on the neural mechanisms involved in music learning, with a basic understanding of the neurobiological mechanisms behind music perception, music learning (skill acquisition), and music production, which will hopefully provide insight into new strategies for the practice and teaching of music.

I am fascinated by educational psychology and cognitive neuroscience within the context of music making and teaching because it requires an understanding of brain networks and states during a task performance. This interdisciplinary research has the capability to inform both music and non-music related educational practices both in and outside of the classroom. To understand the neural underpinnings of music performance, we must understand the general concepts of brain mechanisms. This research introduces a fresh perspective as it is derived from a pianist's perspective in education, an aspect often headed by researchers from alternate domains. Through this translational approach, I aim to discern valuable insights applicable to music academia, potentially enriching our understanding of music making. There seems to be a lack of translation from the scientific community to the educational field, as cited from the Oxford Handbook of Music and the Brain:

> In contrast to the advancing work in music–brain research and music therapy, progress in music education has been much slower. Significant strides in basic research studies in music learning are being made… however, very little has been done in the way of applied research in music education settings similar to the clinical work discussed…" (Thaut & Hodges, 2018, p. 810).

So, how can one use research from the neuroscience and psychology community to increase the expertise of musicians and music educators? More specifically, my questions are:

What is the history of educational neuroscience (including music cognition), what is the current state of music cognition research, and where is it heading? The meat of this discussion invites the following questions: How can we use our understanding of general memory mechanisms to help with memorization of music? Can current research aid our understanding of acquiring, producing, and correcting the most efficient motor movements at the piano? How can we develop more creative individuals with our understanding of research derived from studies on cognition?

Methodology:

This research will be a significant literature review built upon understanding the underlying psychological and neuroscientific components of music making, mostly containing significant articles and studies completed within the last 30 years. Literature will discuss states of learning, creativity, skill acquisition, and flow. The concept of brain plasticity in music has become a part of major scientific studies (Herholz & Zatorre, 2012; Tardif et al., 2016; Wenger et al., 2017) and will be a reoccurring theme throughout several chapters.

The research will also be systematically organized into separate areas of thematic interest. Memorization is also a key component of learning and performing music. Structures such as the hippocampus serve as circuits for memory encoding, storage, and recall (Mehta, 2007; Moscovitch, et al., 2006; Williamon & Valentine, 2002). Therefore, translating an understanding of memorization can be used to create new pedagogical tools and strategies for recall. Utilizing this knowledge, I propose a preliminary framework for potential experiments involving hippocampal spatial and temporal processing which has the potential to translate to music education.

Another chapter will discuss components of motor skill acquisition and possible translations into practical uses for pianists. For example, bimanual coordination of pianists' two hands is an extremely important skill that advanced pianists have a better grasp of than novice pianists (Globerson & Nelken, 2013; Haslinger et al., 2004). Studies show there are interrelated circuits among the motor, auditory, and visual cortices, indicating that teaching practices should include diverse stimuli (Jardaneh, 2017).

In addition, we can recruit the understanding of neural pathways to improve performance both in and outside of the classroom or concert hall. Music encourages brain activity involving spontaneity and flow (Csikszentmihalyi, 2014). As creativity is highly valued in the workplace and daily life, if our understanding of music creation is heightened through understanding neural research, we can utilize these findings to improve solution seeking skills in other disciplines (Araújo & Hein, 2018; Bengtsson et al., 2007).

Current State of Research:

Educational neuroscience, neuroeducation, or "Mind, Brain, Education" is a young field of study that aims to translate the research of neuroscience and cognitive psychology to educational practice and policy (Feiler & Stabio, 2018; Tandon & Singh, 2016; Thomas et al., 2019). Driving collaboration across disciplines, I propose that musical neuroeducation utilizes psychology and neuroscience research and translates them into practical applications for music learning, performance, pedagogy, or even educational therapy.

Though there is research concerning music's benefits for brain health and function (Altenmüller & Schlaug, 2015; Levitin & Tirovolas, 2009; Peretz & Zatorre, 2003), scholarship on transforming scientific findings into practical or applied uses in music making has been less abundant. There have been studies on music's effects on neural plasticity and music processing (Sampaio-Baptista & Johansen-Berg, 2017; Steele & Zatorre, 2018) but there is a gap between researcher, educator, and performer discussing translational applications of scientific findings.

There is a need for a translational discipline to bridge these findings on brain function and apply them to music education settings. My current research is dedicated to understanding what affects these brain states and networks when making music to allow for more informed teaching practices. Finding new directions in piano pedagogy coming from brain-based research will be a great asset to the developing musician, educator, and performer.

Numerous endeavors have been undertaken to dispel neuromyths, including the erroneous belief that only 10 percent of the brain's full capacity is employed, or the misconception surrounding the dominant utilization of the left and right hemispheres (Beyerstein, 1999; Gilstrap 2015). According to Menn and Ledell (2016), regardless of the genesis of these myths, research led by Nobel winners Wiesel and Hubel demonstrated that humans engage nearly the entirety of their brain capacity throughout the day. Employing advanced imaging techniques such as PET and MRI, they monitored oxygen and glucose levels in the brain during various cognitive tasks, such as memory recall, storytelling, or drawing.

The role and unique nature of each hemisphere was originally studied in an experiment by Roger Sperry on split-brain patients, in which their corpus callosum was severed to treat cases of epilepsy. However, phrenology and hemispheric dominance was debunked decades ago (Howard, 2018); the phrase "dominant" hemisphere is a misnomer, according to The Throwing Madonna: Essays on the Brain by William H. Calvin (1991). The term "dominant" in the context of cerebral hemispheres was meant to mean the "language-dominant hemisphere", referring to the location of language processing.

There is also the globally pervasive belief in the VAK (visual-auditory-kinesthetic) myth, which states that if one caters to different styles of learning improvements can be made – However, research indicates that the concept of learning styles is an overly simplistic approach to understanding learning. Most individuals exhibit similar capacities for visual, auditory, and kinesthetic learning. The majority of participants reported using two or three learning styles simultaneously to learn and remember information. Their comprehension and memory were often influenced more by their interest level, level of distraction, and other factors rather than the specific medium used (Krätzig et al., 2006). In fact, music serves as a tool to discover multimodal learning, in which not one style of information processing is focused on; instead, many modes are utilized when encoding new information.

Music's impact on brain structure and functioning, known as neuroplasticity, is evident in the structural and functional differences observed in musicians' brains, particularly in auditory and motor processing (Collins, 2013). Zatorre (2005) emphasizes the complexity of cognitive functions involved in listening to and producing music, showcasing the intricate interplay of auditory pattern processing, attention, memory, motor programming, and sensory-motor integration. Furthermore, music experiences contribute to enhanced performance in perceptual and cognitive tasks, making it a valuable tool for studying brain connectivity and multitasking. The engagement of various brain regions in music, spanning the cortical and subcortical mechanisms of the brain and interconnectivity of the hemispheres, poses a rich area of musical neuroscientific exploration. These findings will hold significant implications for music performance, music education, and the field of cognitive and learning sciences.

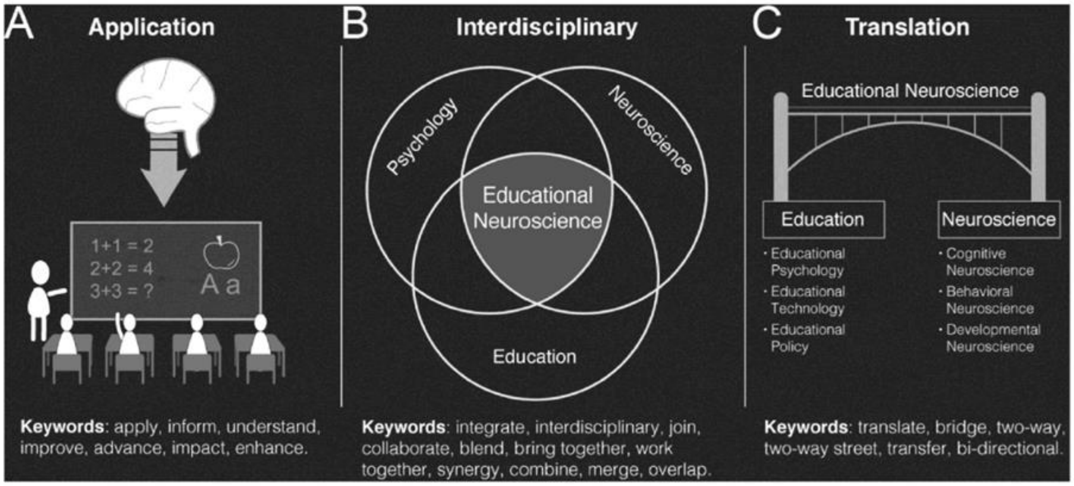
Since the term “neuroeducator” emerged in 1985, coined by Jocelyn Fuller and James Glendening, there has been an upward tick of interest in the intersection of neuroscience and education (Feiler & Stabio, 2018). They envisioned this domain as interdisciplinary in nature, proposing that effective teaching would result from the practical application of knowledge regarding brain structure and function. In turn, this could lead to new discoveries about learning and brain function. This burgeoning field has been referred to as either educational neuroscience, neuroeducation, or Mind, Brain, and Education. Feiler and Stabio (2018) highlight that educational neuroscience extends beyond merely improving or analyzing teaching methods. It aims to understand how students learn, how learning alters the brain, and how these insights can be applied in the classroom. The authors outlined three foundational pillars and thematic areas represented evident in the seminal literature of neuroeducation:

> Each definition in the literature fell broadly into one of three major themes: definitions that focus on the application of neuroscience into the classroom to improve educational practice, definitions that focus on collaboration or integration of multiple disciplines, and definitions that focus on bridging or translating language from different disciplines. (Feiler & Stabio, 2018, p. 18)

Feiler explains the first theme has the potential to "improve educational practices", which can be referred to as translational science. The second is based on the idea that the "whole is greater than the sum of parts", in which collaborative efforts across disciplines facilitate a seamless transition between different fields and promote the examination of complex questions through multi-level analysis. Distinct methods, paradigms and specialized terms have traditionally been confined into separate domains – however, the aim is to build a connection between the technical jargon of neuroscience within the scientific community to make this accessible for educators and extending this to educational policy makers. The authors further elaborate, "when we consider the potential of neuroscience to actually inform the public in realms such as language development, literacy, mathematics, and social and emotional development, there is substantial promise" (Feiler & Stabio, 2018, p. 22). I extend this principle to the idea of integrating music education, psychology, and neuroscience into an interdisciplinary field helping students and teachers learn.

Figure 1

Three foundational pillars of educational neuroscience



Note. From "Three pillars of educational neuroscience from three decades of literature" by Feiler & Stabio, 2018, *Trends in Neuroscience and Education, 13*, 17-25.

Lastly, they propose a working definition for educational neuroscience:

> The integration of education, psychology, and neuroscience into an interdisciplinary field that is devoted to helping students learn. Educational neuroscience communicates the language of multiple disciplines and applies methods from multiple disciplines to translate discoveries about the brain and its networks into educationally relevant outcomes (Feiler & Stabio, 2018, p. 23).

Thomas et al. (2019) explores the origins and primary research areas within educational neuroscience, alongside the challenges inherent in this interdisciplinary and translational field. Since its inception, new academic journals have been established such as The Trends in Neuroscience and Education, Mind, Brain and Education, and Educational Neuroscience. The authors of this paper emphasize that psychology is not sufficient (we also need neuroscience) because while psychology examines the impact of instruction on behavioral changes, whereas neuroscience investigates brain mechanisms underlying those changes in behavior.

Outlined in a study by Pincham et al. (2014) is a practical four-step approach detailing how educational neuroscientists can contribute to classrooms and practically apply neuroscientific knowledge. By following this approach, new scientists will be empowered to enhance the bridge between education and neuroscience. Furthermore, the authors emphasize that "this metaphorical highway reflects the notion that educational neuroscience can no longer be thought of as a mere bridge connecting two existing fields but must be afforded the status of an autonomous discipline" (Pincham et al., 2014).

Primary concerns in this discussion revolve around *whether* understanding how the brain functions is applicable to educational methods, and if so, *how* neuroscientific discoveries can be effectively integrated into classroom setting. The first step in their paper claims that researchers and teachers should work together to identify an educational need, studying the existing literature and identifying insights that neuroscience can contribute. The second is to develop a research proposal, test this in the classroom, and then communicate and evaluate the results together. The last steps include in-classroom testing as well as reflecting on findings.

Meltzoff et al.'s paper (2009) illustrates that in human learning, what separates homo sapiens from other species is our ability to make abstractions from experience in learning new skills. For instance, infants have a strong fascination with the behaviour of other humans and utilize implicit learning mechanisms in their social interactions. In their paper they outline three principles that have been emerging from cross-disciplinary research across psychology, neuroscience machine learning, and education. The first is that “learning is computational” – meaning, young children have strong inference or computational skills that enable them to automatically infer models of their environment based on the statistical patterns they have already experienced – they use statistical patterns taken from experience to learn language and cause-effects relationships. The second is that “learning is social” – infants are prone to imitating the behaviors of others. Machine learning studies indicate that when a robot displays social-like behaviors, children are more inclined to pay attention and learn from it. The third is that “learning is supported by brain circuits linking perception and action”. The paper outlines how “newborns as young as 42 minutes old match gestures shown to them, including tongue protrusion and mouth opening. This is remarkable because infants cannot see their own faces, and newborns have never seen their reflection in a mirror. Yet, newborns can map from observed behavior to their own matching acts, suggesting shared representations for the acts of self and others” – therefore,

> Social learning, imitation, and sensorimotor experience may initially generate, as well as modify and refine, shared neural circuitry for perception and action. The emerging field of social neuroscience is aimed at discovering brain mechanisms supporting close coupling and attunement between the self and other, which is the hallmark of seamless social communication and interaction (Meltzoff et al., 2009, p. 285).

In terms of student-teacher learning, this illustrates that demonstrative learning is still extremely important. Mirror-neurons are at work while watching hand movements of other pianists even while the observer is not playing.

As well, human language learning demonstrates the crossover between computational learning, social learning, and shared neural circuitries. For example, in an experiment where infants were exposed to a foreign language, these babies learned phonemes better when only exposed to a human being, but not when shown or hearing the phonemes from a TV (Kuhl, 2010). This kind of imitation learning is also found in other species - passerine birds, for example, learn bird calls and bird songs by observing and imitating adult birds. Similar to humans, young birds listen to adult conspecifics sing during a critical period in their development and then practice these songs during a "sub-song" phase, similar to babbling in humans, until they are perfected. Neural models of birdsong learning can explain this gradual process of iterative improvement. Additionally, just as in humans, a social environment plays a crucial role in enhancing vocal learning in birds.

Brain Imaging and Electrophysiological Tools:

When examining brain activity, researchers typically employ three methodological approaches. The first involves analyzing the electrical activity of neurons. Both EEG (electroencephalography) and MEG (magnetoencephalography) record and measure electrical currents, while MEG also detects magnetic fields. The second method alters the excitability of neurons to investigate brain function. This is achieved by stimulating neurons externally using magnetic pulses in TMS (transcranial magnetic stimulation). Alternatively, tDCS (transcranial direct current stimulation) applies repeated pulses to the scalp, either inhibiting or activating large networks. The third method measures cerebral blood flow, analyzing the oxygen and glucose levels that vary depending on the consumption of neuronal cells. For example, fMRI, functional magnetic imaging, detects changes in blood flow and oxygenation levels in the brain that occur in response to neural activity. When a specific brain area becomes active, it requires more oxygenated blood. The fMRI machine measures these changes by tracking the magnetic properties of blood as it flows through different regions of the brain. By analyzing these changes in blood flow, researchers can create detailed maps of brain activity associated with various tasks or stimuli. Each methodology and neuroimaging method has its own strengths.

Electrophysiological methods such as EEG and MEG offer exception temporal resolution and can display in detail the “when” of neurons are firing. These methods can also reveal cell assemblies involved in information exchange, facilitating connectivity analysis to demonstrate coherence between difference cell assemblies. In contrast, other neuroimaging methods such as fMRI and PET (positron emission tomography) are good for longitudinal studies, which show the “where” of cells firing, and is an excellent method for showing brain changes over time. Therefore, methods such as fMRI imaging are sufficient for spatial resolution, allowing specific tasks or skills to be related to certain brain structures. However, fMRI and PET lack temporal resolution (seconds to minutes), making real-time tracking of cell firings difficult unlike in EEG or MEG methods. The neuroimaging methods are also far more costly than EEG, TMS, and tDCS. Diffusion Tensor Imaging (DTI) is a neuroimaging technique used to visualize the white matter tracts in the brain. It measures the diffusion of water molecules along these fiber pathways, providing insights into the structural connectivity of the brain. DTI can map out the direction and strength of diffusion in three-dimensional space, allowing researchers to infer the integrity and organization of white matter tracts. This information helps in studying conditions where changes in the brain's structural connectivity may occur, such as in neurodevelopmental disorders or brain injuries.

Basics of Brain Mechanisms for Learning

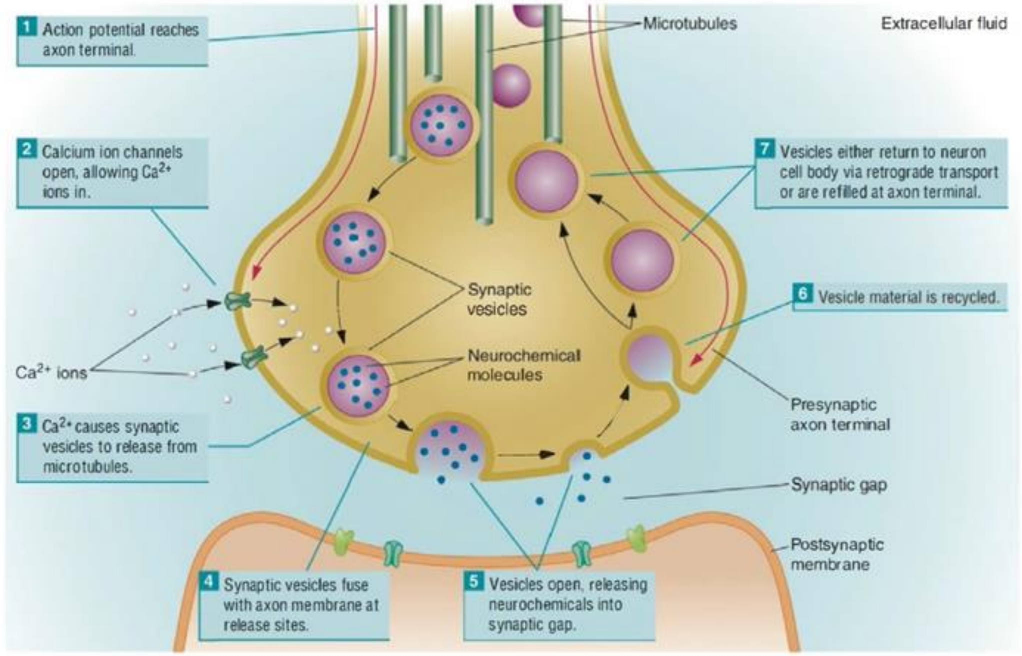
Neuron Structure and Function

The nerve cell, or neuron, is composed of its cell body (the soma), which houses the cell's nucleus, DNA and genetic material. The basic prototype of a neuron composes of the soma, the dendrites, axon, and axon terminals. The dendrites receive incoming information, which is then interpreted in the soma. Through the axon hillock this information is electrically transferred through the axon via an action potential. The actional potential culminates at the axon terminals, which causes the release of neurotransmitters into the synaptic cleft. The release of these neurotransmitters is picked up by the dendrites of another cell, and the process is repeated. The axon is also covered by a myelin sheath which is formed by oligodendrocytes, a type of macroglial cell in the CNS, and Schwann cells that form myelin sheaths in the PNS.

At the neuron's axon terminals, neurons communicate with other neurons at the synapse, located between axon terminals and dendrites. The space between the two neurons is called the synaptic cleft, which is microscopically small, from 40nm wide (a human hair is about 75,000 nm). The synapse is composed of the presynaptic and postsynaptic neuron – when an action potential occurs and reaches the axon terminal, calcium Ca2+ ion channels will open allowing calcium ions into the presynaptic neuron. The influx of calcium causes the release of synaptic vesicles (carrying neurotransmitters) from microtubules. The vesicle, full of neurotransmitter molecules, will fuse into the presynaptic membrane, which will release the molecules into the synaptic gap. These neurotransmitters may bind to receptors in the postsynaptic cell, which can potentially cause another action potential to occur, or decrease the potential for an action potential to fire. Over time, neurotransmitters lingering in the synaptic cleft will disperse through diffusion. Alternatively, they may undergo reuptake, where they are reclaimed by the presynaptic neuron for later use, or they might be transported back to the cell body via retrograde transport. On the postsynaptic side, neurotransmitters will bind to receptor sites found on membrane proteins, each receptor site only responding to certain types of neurotransmitters. These ionotropic receptors, located on these ion channels, are also called ligand gated ion channels that open quickly or slowly (metabotropic). When ligands (the neurotransmitters) bind, the ion channel reconfigures to let in ions. The postsynaptic neuron will have two outcomes – it will undergo excitation, which increases the cell's ability to create an action potential, or it will get an inhibitory response, a decrease in likelihood of generating an action potential.

Figure 2

The synapse



Note. This figure illustrates calcium entering the presynaptic cell and the resulting release of neurochemicals into the cleft. From *Discovering behavioral neuroscience: an introduction to biological psychology* by L. Freberg (2016).

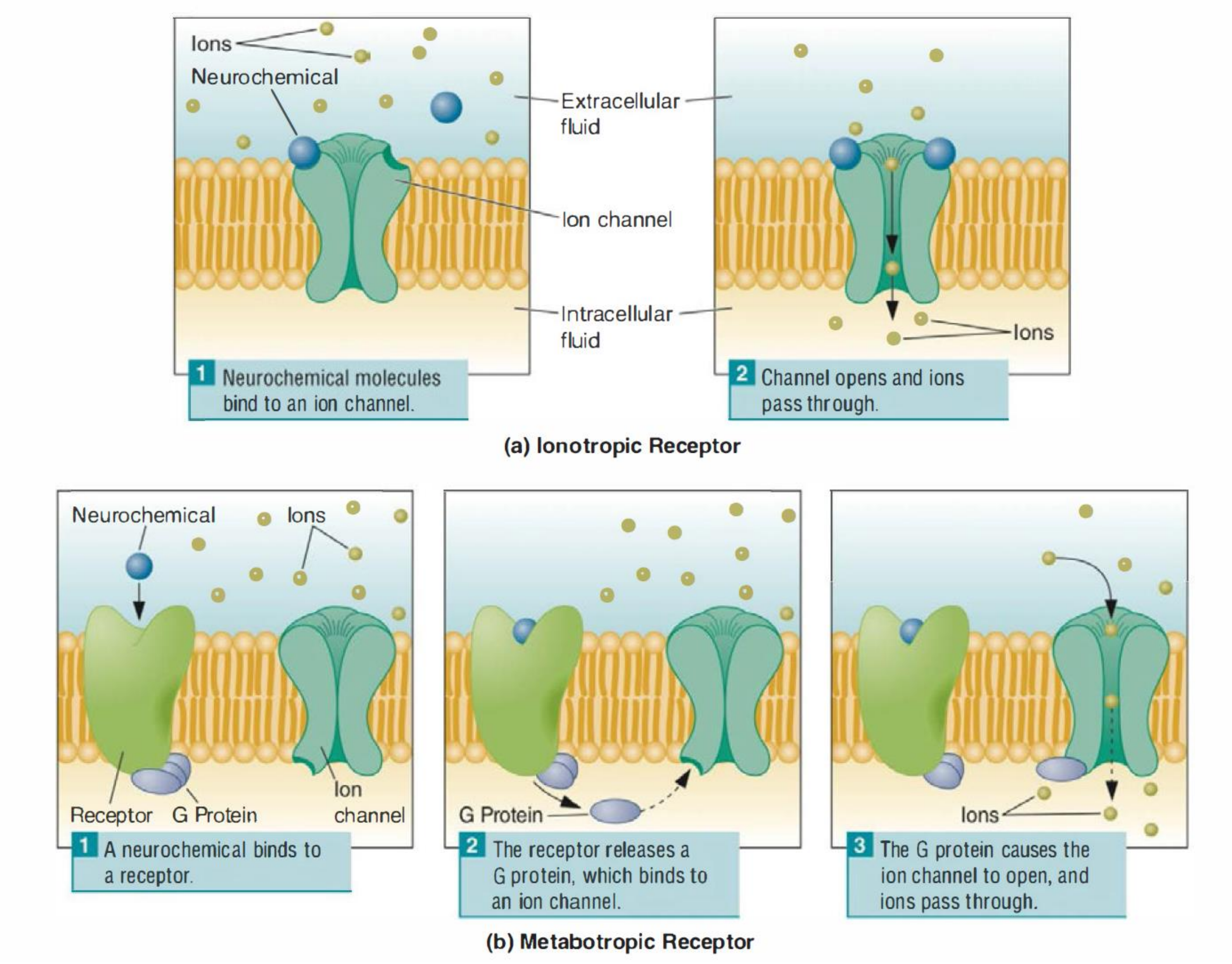
Membrane and Action Potential

Before discussing action potential, we have to discuss membrane potential. The neuron membrane is composed of a biphospholipid layer, as well as protein structures that function as ion channels, allowing ions to travel through without using energy, or ion pumps which require the use of energy. These ion channels can be voltage-dependent, which will allow or not allow ions through depending on the electrical charge surrounding the membrane. Another type of ion channel is ligand-gated channels, which are activated by the binding of certain neurotransmitters to the protein structure. There are also two main types of ion pumps (that use energy). These are sodium-potassium pumps (pump out 3 Na+ ions from the cell when it takes in 2 K+ ions), and calcium pumps which release 2 Ca2+ ions. Changes in membrane potential typically occur at the axon hillock and along the axon, which initiates an action potential using voltage gated ion channels (Na+ and K+). Membrane potentials also change at dendrites and axon terminals, though those are typically due to ligand-gated channels.

There are certain types of ions that are important for membrane potential. Sodium Na+ ions, and chloride Cl- ions, which are in higher concentration outside of the cell when the cell is at rest. There are also potassium K+ ions, which are also higher in concentration inside (intracellular fluid) than outside of the cell (extracellular fluid) at rest. There are also other organic anions (negative charge) inside the cell as well. At rest, the inside of the cell is also overall more negatively charged than the outside of the cell, which means the average neuron will have a resting potential of about -70 millivolts (mV). To keep the membrane potential negative, this is maintained by the sodium-potassium pump, which as stated uses energy to pump out 3 Na+ ions, and also pumps in 2 K+ ions into the cell. Meanwhile, K+ ions are always moving freely across ion channels, in which these K+ ions will be freely cross the resting membrane until forces (like diffusion, because of concentration gradient) won't move it in either direction, maintaining the negative membrane potential. The membrane is permeable to potassium, and a bit for sodium ions (leakage). So, resting potential is dependent on both the equilibrium of concentration of ions (diffusion), but also the electrostatic pressure (positive or negative charge) of the membrane.

Figure 3

Neurochemicals binding to protein receptors sites



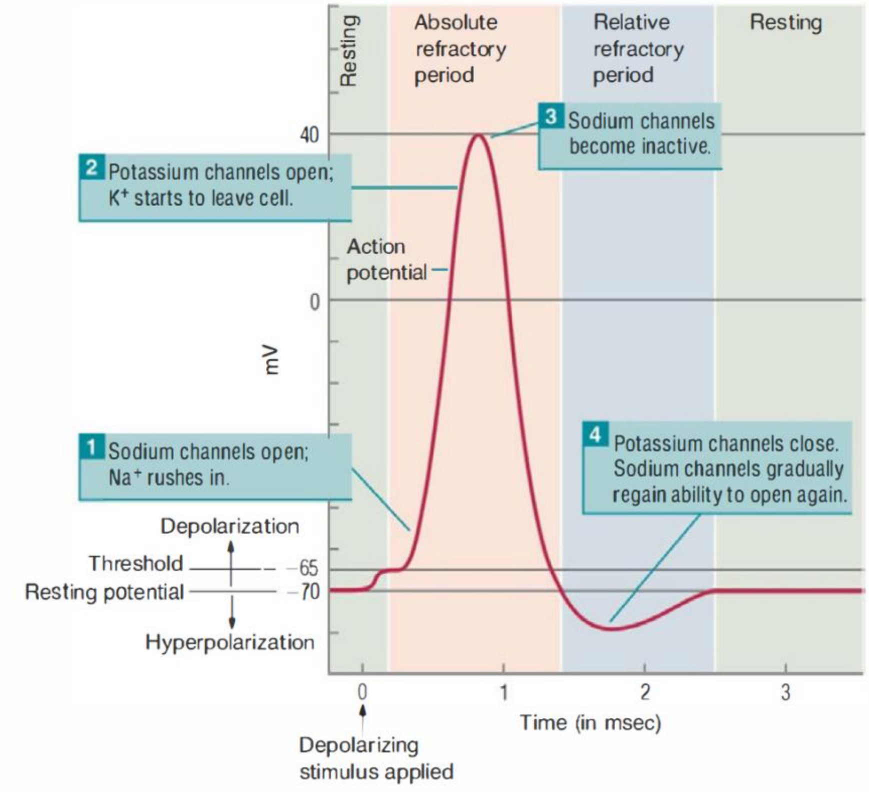
Note. From *Discovering behavioral neuroscience: an introduction to biological psychology* by L. Freberg (2016).

Synapse study and plasticity

How action potentials occur – when neurotransmitters bind to receptor sites of the dendrites of a postsynaptic neuron, it can cause the membrane (resting at -70mV), to depolarize, meaning it will become more positive. The neuron will sit at resting state, reach its threshold potential (around -55mV) and then reaching this threshold will allow voltage dependent Na+ ion channels to open, allowing a rush of positive Na+ ions to come into the cell. This causes depolarization in the cell, until the membrane potential crosses zero and becomes positive, known as the rising phase. This rush of positive ions causes the electrical signal, the action potential, which travels down the axon. Eventually the peak of the action potential will be reached, signaling Na+ ion channels to close, and K+ ion channels to open to get rid of extra positive charge. The falling phase, or repolarization, is due to the potassium ions finally exiting the cell. However, there is a brief period where the cell is hyperpolarized (there is too much negative charge), called the refractory period. Hyperpolarization occurs because K+ channels close slower than the Na+ ones, releasing more potassium ions than necessary. Eventually the potassium channels fully close and it will return to resting potential. The propagation of myelinated axons is known as saltatory conduction, in which the action potential "jumps" from one Node of Ranvier to the next node.

Figure 4

Action potential



Note. From *Discovering behavioral neuroscience: an introduction to biological psychology* by L. Freberg (2016).

This process occurs for action potentials at the axon hillock and propagated along the axon, but what about at the synapse? Well, when neurotransmitters (ligands) bind to postsynaptic receptors, there is excitation or inhibition. When Na+ enters the postsynaptic side, a small depolarization occurs, perhaps up to -60nm, in which this is called the excitatory postsynaptic potential (EPSP), which increases the excitability and probability an actional potential will fire in this cell. These EPSP's occur because of ligand gated channels, not voltage-gated channels for action potentials. If chlorine Cl- enters the cell, this hyperpolarization of the postsynaptic cell is called inhibitory post synaptic potential (IPSP). Both of these responses last

5-10 ms. Most dendrites and spines will receive excitatory input, while synapses on the cell body will typically receive inhibitory input. When receiving these inputs, the cell undergoes neural integration, rapidly spreading the EPSP or IPSP to the axon hillock, deciding whether an action potential should be fired or not.

Referring back to Hebbian neuroplasticity mechanisms…Donald Hebb in the 1940's stated that learning involves strengthening and reinforcement of specific neural connections, which led to the phrase "neurons that fire together wire together". This process entails the encoding of spatial and temporal patterns during learning, thereby forming distinct memories. In other words, if a presynaptic neuron repeatedly and persistently stimulates a postsynaptic neuron, the connection between them is reinforced, leading to enhanced communication. Conversely, if presynaptic activity lacks corresponding postsynaptic firing, the synaptic connection weakens. The modification and strengthening or weakening can be explained through Hebbian plasticity, which is thought to underlie various forms of learning and memory, as well as the development and refinement of neural circuits during brain development. LTP (long term potentiation) represents a long-lasting change in synaptic strength that results from repeated and persistent EPSPs (excitatory postsynaptic potential), reflecting the cellular mechanisms underlying Hebbian plasticity. LTP is a process by which the synaptic connections between neurons become stronger when continuously activated. Essentially LTP is a form of synaptic plasticity characterized by the long-lasting strengthening of synaptic connections between neurons. It is typically induced by high-frequency stimulation of a presynaptic neuron, leading to the repeated firing and release of neurotransmitters at the synapse.

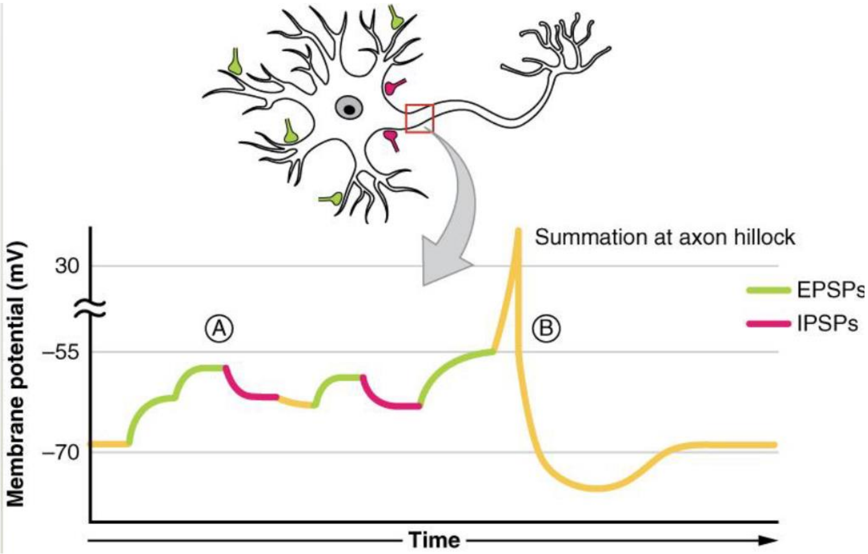
EPSPs are transient changes in membrane potential that occur in the postsynaptic neuron in response to the release of neurotransmitters (such as glutamate) from the presynaptic neuron.

Glutamate can bond to several different kinds of receptors. AMPA, NMDA, and kainite are three types of ionotropic glutamate receptors. In STP (short term potentiation), glutamate bonds to an AMPA receptor on the postsynaptic side, which allows Na+ ions to flow through. The NMDA receptor allows Ca2+ ions to enter as well, which strongly depolarizes the membrane potential. In eLTP, more AMPA receptors are moved into the membrane, allowing for more glutamate to bind and cause more ion flow, and dendritic spines are enlarged. For lLTP, BDNF is released to stabilize the excited synapse – the BDNF release TrkB receptors on both pre and post synapse sides, increasing everything that has already been happening, amplifying the response of the synapse for future input. LTP can be increased by neuromodulators, such as dopamine. Homeostatic plasticity maintains the stability and balance of neural circuits. These two forms of plasticity work together to shape the functional properties of neural networks and support adaptive responses to changing environmental demands.

Neuromodulators, such as dopamine, can affect the E/I balance long before an action potential is even fired. We are used to seeing the textbook version of what action potentials look like (above). However, at resting potential the indicated line should be better represented as a fluctuating line, polarizing or depolarizing and eventually firing. For example, if the neuromodulator dopamine is already affecting the neuron, the cell will already be experiencing a slight depolarization, creeping closer to its threshold. GABA will do the opposite. If the resting potential is elevated beforehand, it requires less stimulation to trigger an action potential before it occurs. In a sense, this has already been priming for an action potential to occur.

Figure 5

Neuromodulators aid action potential



Note. From Implantable Low-Noise Fiberless Optoelectrodes for Optogenetic Control of Distinct Neural Populations by K. Kampasi, 2017.

Reward, Oscillations, and Entrainment:

Listening to or producing higher order pleasures such as music are suggested to derive from similar neural mechanisms as food, sex, and drugs – more specifically, regions such as the vmPFC, OFC, ventral striatum, and amygdala (Blood & Zatorre, 2001). The similarity here is that dopamine cells fire after receiving a reward, but also fire with cues that are associated with the reward or that predict a reward. It seems that music activates the same dopamine activation reward system. Because the brain has strong predictive functions and an innate focus on recognizing patterns (required biologically for survival), the brain tends to also code for anticipation and expectation. The brain is driven by analyzing the statistical regularities of incoming auditory information. Even among infants, research has demonstrated that exposure to rhythmic beats can evoke changes in brain activity, particularly when irregularities like a missing beat occur, as evidenced by event-related potentials (ERPs) signaling the brain's detection of the mismatch (Nederlanden et al., 2018). Unpredictability can also lead to pleasure, and the response to prediction error is mitigated by dopamine and endorphins.

Another aspect of music is neural entrainment, which could be the underlying mechanisms behind behavioral entrainment (dancing, etc.). Neural entrainment is the process of synchronizing the neural oscillations to external rhythmic stimuli or the process of frequency coupling across different brain regions. When people listen to enjoyable music, EEG scans show greater strength in all frequency bands. Entrainment exhibits more distinct patterns, particularly with lower sound frequencies like a low bass, which tend to engage sensory-motor regions more prominently, often leading to finger or toe-tapping. Nozaradan's paper (2014) demonstrates how the brain synchronizes to auditory oscillations or frequencies of sounds – they recorded EEG signals from the frontal lobe, in which the brain's oscillations were found to match the frequency of the sound oscillations provided – the EEG amplitude (referring to the number of neurons firing, the populations of neurons firing). An interesting finding was that even if the auditory input was stopped, the beat pattern persisted, suggesting the brain remembered the oscillation frequency and repeated it.

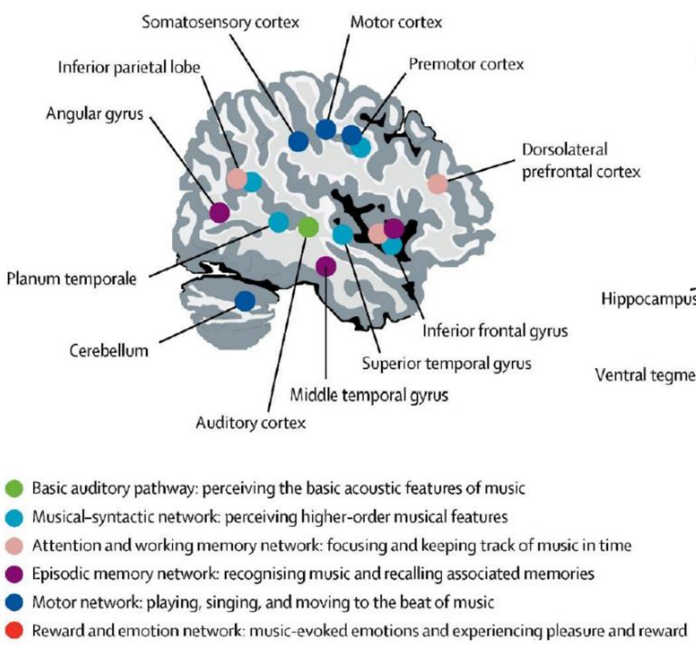
Through the auditory system, beat integration is combined with other sensory inputs, which is interesting because sensory inputs can be modified through other stimuli such as visual inputs (like watching a conductor). Luck & Sloboda (2008) exhibit that visual beat perception is signaled by acceleration/deceleration, rather than up, down, or side to side changes in direction. Moreover, their studies displayed that acceleration in the vertical motion along the gesture's trajectory communicated beat placement more effectively, therefore increasing synchronization with the ensemble. Luck and Sloboda describe this phenomenon:

> A large change in direction (small radius of curvature) will be accompanied by a larger change in speed compared to a small change in direction (large radius of curvature). Thus, if changes in speed(a) offer the main cue for synchronization, manipulation of the radius of curvature with which the beat is defined will impact upon the clarity of this cue, and thus its identification (Luck & Sloboda, 2008, p. 470).

Keller et al. (2014) offered insight into the internal processes and mechanisms that enable rhythmic coordination with others. The authors' theory of successful interpersonal coordination involving three core cognitive-motor skills appears to also correlate to beat induction and perception - "Anticipation, attention, adaptation. These three are influenced by the performer's goals concerning the interaction, their knowledge about the music and familiarity with co-performers, use of regulatory strategies to facilitate coordination, and social-psychological factors (e.g. personality)" (Keller et al., 2014, p. 2). One of the first issues mentioned was a remark in Serrano (1993) about musicians being able to anticipate the beat – if the conductor can induce beat perception, the observer should anticipate actions through mental images, or "activating memory representations of shared goals." I think this statement speaks to why synchrony in ensemble music making is highly worked on and emphasized: "At the level of the brain, rhythmic coordination can be used to promote neural alignment, which could improve joint action, communication, neural efficiency and thus social bonding" (Keller et al., 2014, p. 8). The inclusion of visual cues improves beat perception, as evidenced by EEG results. This parallels language acquisition, where visually observing someone speak enhances auditory comprehension of spoken words. The ability to integrate multiple sensory inputs begs us to ask the question, what is common between these networks, and if there is overlap in networks between music and language processing, could this understanding be utilized in therapeutic environments involved in language disorders or neurological conditions?

Figure 6

Key processing areas for language and music



Note. From “Music-based interventions in neurological rehabilitation” by Sihvonen et al., 2017.

Loui et al. (2019) state:

> On one hand, we see that musical sounds provide an optimal stimulus set with which to understand the fundamental properties of attention, executive functions, and creativity. On the other hand, music also offers a window through which researchers may assess effects of long-term training on more general cognitive function, as well as neurocognitive development throughout the lifespan (Loui et al., 2019, p. 263).

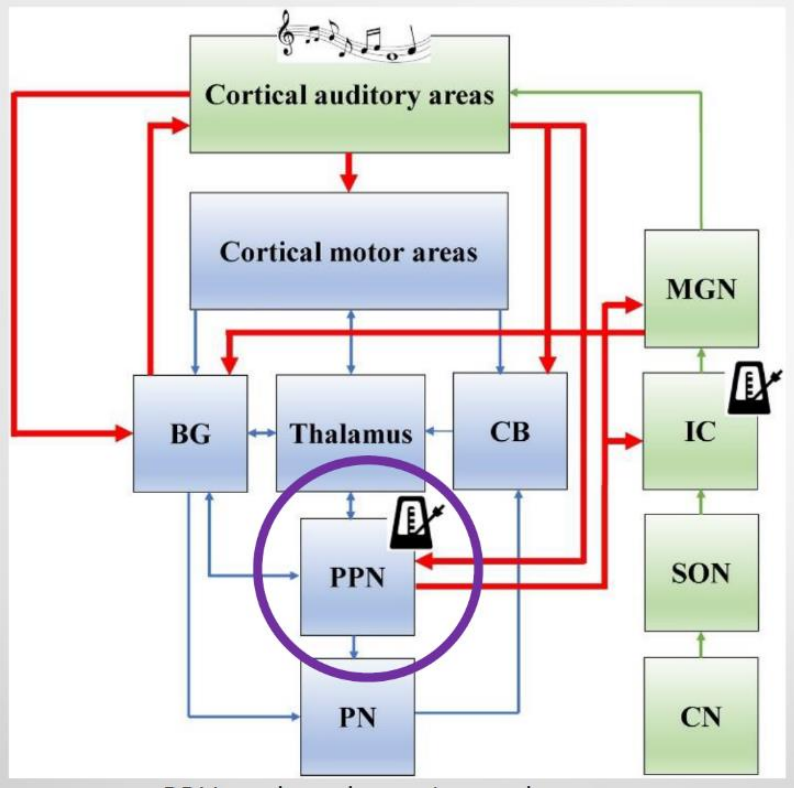
The study of rhythmic attention is increasingly linked to brain rhythmic oscillations, a concept dating back to the 1800s and notably advanced by Hans Berger in the 1920s. Berger identified the alpha rhythm, dominant during relaxation, through EEG, highlighting the brain's intrinsic rhythmic fluctuations. Research indicates that different brain rhythms, such as beta, gamma, and delta, correspond to various mental states and are crucial for neuronal communication. For instance, beta activity, associated with motor areas, plays a key role in processing rhythmic music and coordinating rhythmic attention through the auditory and motor systems.

Recent studies indicate that musical rhythm guides auditory attention through the entrainment of brain oscillations across various frequencies, involving both the motor and auditory systems. This mechanism not only aids in processing musical rhythms but also influences how the brain handles speech rhythms. Understanding these neuronal rhythms and their entrainment could lead to music specifically designed to enhance attention, using rhythmic elements that align with certain brain frequencies to boost cognitive functions. Such insights are promising for developing music-based therapies aimed at training attention and executive functions effectively.

Sihvonen et al. (2017) illustrate the impact of musical therapy on stroke or aphasia patients. Over a period of 0, 3, and 6 months, MEG responses revealed heightened activity in patients who listened to music compared to both a control group and a group exposed to audiobooks. Music intonation therapy (MIT) has also been utilized to help stroke patients with producing speech. As well, DTI studies have found that MIT treatment has increased the white matter pathway (more specifically the arcuate fasciculus) connecting Broca (frontal lobe) and Wernicke’s area (temporal lobe), demonstrating the areas that MIT have changed and that are related to producing and understanding language. Additionally, music has been profound in Parkinson’s and Alzheimer’s (dementia) research. Koshimori & Thaut (2018) investigated the effects of neural entrainment and beat patterns with behavioral entrainment. Their patients with Parkinson's disease experienced difficulties walking; however, the rhythmic patterns of music aided them in regaining their ability to walk again – how is this possible? The stimulus, music, provided rhythmic cues to the system so that it could produce motor responses.

Figure 7

Degeneration of the PPN in Parkinson’s patients



Note. IC: inferior colliculus. PPN: pedunculopontine nucleus (the primary nuclei - cluster of neurons - for acetylcholine production in the brainstem, in the pons/midbrain areas - projects to the basal ganglia. PPN: pedunculopontine nucleus - detects gait and movement rhythmic patterns. From Future perspectives on neural mechanisms underlying rhythm and music based neurorehabilitation in Parkinson’s disease by Y. Kimoto and S. Furuya (2019).

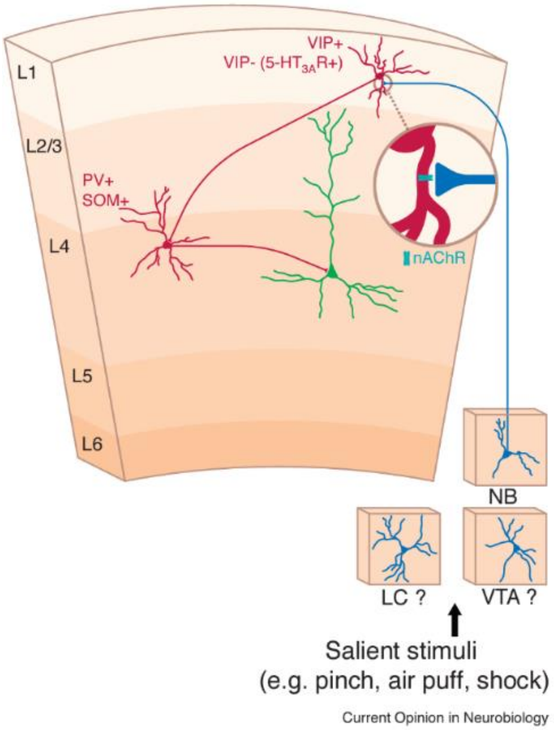
The PPN sends information into the motor areas as well as downstream into the spinal cord which engages movements. With Parkinson's there is a loss of dopamine in the substantia nigra (in the midbrain which is part of the brainstem) and neurodegeneration of the PPN. The PPN is analogous to a metronome, aiding in the regulation of timing and rhythmic bodily movement. It is involved in the control of posture, locomotion, and the initiation of movement, and it plays a role in synchronizing various neural circuits involved in motor control. Therefore, PPN dysfunction PPN leads to disturbances in gait and movement coordination. When the PPN is not functioning normally, music therapy can play an integral role – the beat pattern, or oscillations of the music arrive via the IC (inferior colliculus, part of the midbrain and part of the auditory pathway) which are sent to the cortex, which is sent from the auditory to motor areas, which affect the beat and rhythm of walking.

There have also been studies done testing if music beat patterns can be used therapeutically to treat memory disorders, such as patients with Alzheimer's and dementia. It is well known that amyloid beta and tau proteins are one of the hallmarks of Alzheimer's. In their 2016 study, Klein et al. conducted research using mice engineered to accumulate certain proteins. They observed that in mice with Alzheimer's disease, the hippocampus exhibited significantly lower oscillation frequencies compared to healthy mice. This decrease in gamma rhythms was attributed to the disruption caused by amyloid beta proteins. An MIT lab (Iaccarino et al., 2016) stimulated the hippocampus of these mice (using optogenetics) with light frequencies, at 40 Hz, decreasing amyloid beta by about 50 percent. They discovered the inflicted gamma frequencies activated glial cells to start scavenging, enhancing protein clearance (remembering genes drive what proteins are made, but proteins drive the action/inaction of the cell). More studies are being done to study gamma and ways to apply this noninvasively.

Examining the neural circuits associated with attention, they are traced back to the basic auditory pathway, in which auditory information passes through the thalamus (which houses the medial geniculate nucleus, MGN) before projecting to the auditory cortex. The processing of attention salient information ultimately enhances information processing in the auditory cortex, which strengthens the thalamus to auditory cortex connection – Patton et al. (2019) describes this process in their paper: In the basal forebrain there is another structure called the nucleus basalis (NB), which has the largest collection of acetylcholine neurons in the brain projecting to multiple areas of the cortex. When salient external stimuli accompany auditory information (such as finger pointing), the NB and its ACh neurons are activated. These ACh neurons project up to the interneurons of the auditory cortex. The ACh neurons release excitatory acetylcholine neurotransmitters that bind to acetylcholine ionotropic receptors (nicotinic ACh receptors) of the interneuron, which instigates a firing of the first interneuron to synapse to the next. These interneurons, each release inhibitory GABA (gamma-aminobutyric acid), and the release of further GABA from subsequent synapsed interneurons leads to disinhibited neurons in the auditory cortex, which leads to a higher chance of firing when more glutamate is released from the thalamus. This results in a larger response in the auditory cortex. Therefore, this demonstrates that salient attentional stimuli can invoke higher thalamus to cortex connections, aiding in language learning, and possibly music learning.

Figure 8

Attention salient stimuli circuitry



Current Opinion in Neurobiology

Note. From “Rejuvenation of plasticity in the brain: opening the critical period” by Patton et al., 2019.

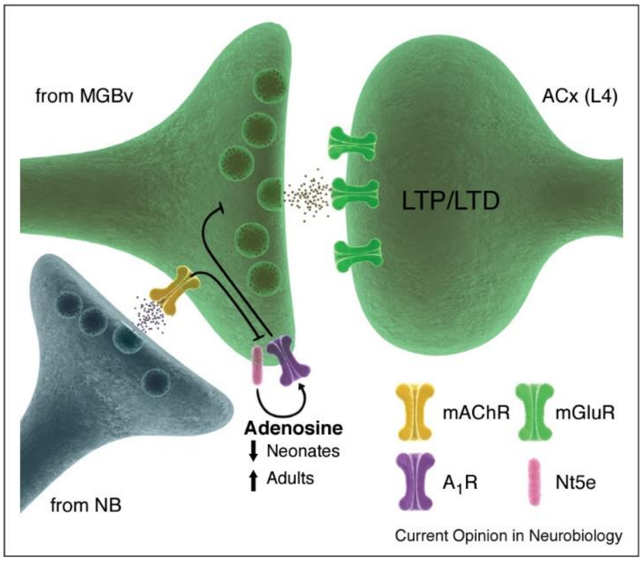
Critical Learning Period:

There is also discussion regarding the existence of critical periods of neuroplasticity for learning, a concept that can extend to the realm of music. Numerous studies in language acquisition have demonstrated that neural circuits responsible for detecting speech patterns and irregularities are established within the first year of learning. For example, phonetic discrimination in one’s native language earlier in life predicts word production later in life (Kuhl, 2010). As well, during the early critical periods, language acquisition is supported by social interactions – Kuhl (2010) conducted a comparison of American infants exposed to a non-native language, Chinese, vs. American infants exposed to English. She exposed them to a non-native language in person (live), via television, or through only audio. The study revealed that infants exposed to Chinese in person exhibited enhanced phonetic discrimination of a non-native language after 12 sessions, achieving results comparable to those of infants raised in a Chinese-speaking household. This demonstrates the importance of live interactions, but also the learning capacity of infants that are only 9 months old. Live interactions were better because of social cues (pointing, social gaze like attention). So, language learning evolved from the brain's tendency to detect statistical regularities as a means to make future predictions. What's going on in neural networks that facilitate this learning? It seems as if plasticity mechanisms (Hebbian/homeostatic) factor in during the first months to a year, when there is an extreme amount of synaptic pruning. Kuhl (2010) claims that second language learning has "critical periods" of learning – we have to look at neural circuits to explain this critical period.

Patton et al. (2019) describes the causes of this critical learning period with a thalamic adenosine hypothesis. Recall attention signaling involving the nucleus basalis and the auditory cortex, with nicotinic ACh receptors disinhibiting auditory cortex neurons leading to ease of firing caused by glutamate. Notably, the nucleus basalis also projects ACh neurons to the presynaptic terminals of the auditory thalamus (MGN). However, instead of activating nicotinic receptors, the ACh binds to mAChR (metabotropic muscarinic cholinergic receptors) in the auditory thalamus. These metabotropic receptors have an indirect effect on the process through adenosine receptors. Adenosine retains vesicles of glutamate inside the cell, thus when activated, its role is to inhibit the release of GLU from the vesicles. During the sensitive or critical period of learning, the mAChR receptors shuts off or inhibits the adenosine, which in turn causes the release of glutamate from the vesicles. Therefore, the release of acetylcholine that triggers adenosine inhibition (“turn off” adenosine) is effectively "disinhibiting" the thalamus, leading to increased release of the glutamate neurotransmitter. When greater glutamate is present, this leads to higher LTP, resulting in greater excitability of the auditory neurons, thereby increasing the sensitivity of information processing. After the release of GLU, at the thalamic-cortical synapse the mGluR (metabotropic glutamate receptors) on the postsynaptic cell receive glutamate – because it is metabotropic, the effects of LTP are long lasting. The closure of the critical period occurs when acetylcholine binds to mAChR. But instead of deactivation, adenosine becomes activated, which retains glutamate (GLU) vesicles, resulting instead to long-term depression (LTD). The metabotropic LTD lasts much longer than LTP activated by NMDA receptors. When this critical period closes, the pyramidal cells of the auditory cortex have a much higher firing threshold, so passive auditory information becomes much harder to activate the LTP process.

Figure 9

Thalamic adenosine hypothesis



Note. “Rejuvenation of plasticity in the brain: opening the critical period” by Patton et al., 2019.

This likely explains why in children, effortlessly absorbing information is akin to being a "sponge," whereas in adulthood, this process is not as seamless, signifying a shift in learning ease. Essentially, neurons become more selective and optimized for incoming auditory stimuli. So, this leads to the conversation of why adults have a harder time learning new languages or skills. As adults, neurons undergo neural entrenchment, a process whereby computations or information become efficiently engrained. Consequently, integrating new information becomes difficult, imposing constraints on later learning in adulthood when processing areas have already been established.

Another type of constraint is the learning systems available to children vs adults. For children, it has been studied that implicit (procedural) memory systems are more dominant, whereas starting from teens to adults the explicit (declarative) memory system is more utilized (Meltzoff et al., 2009). For procedural memory, we understand it as the “how” of doing a task, based on implicit understanding of rules and habits – this is a slow process, making incremental improvements that require much repetition, reinforcement, and feedback. As for adults, this explicit memory system utilizes more verbalized and transferred knowledge, utilizing working memory and executive functions – this is not fully developed and available in young children. In this explicit process, there is also an inhibition of procedural memories - for instance, when playing an instrument such as the piano, articulating the execution process (the “how” of playing) may lead to momentary confusion with playing, hindering the ability to perform intuitively and automatically as done before. Explicit thinking disrupts the automated, habitual movements of piano playing – the procedural memory movements. Alongside the use of learning strategies, this explicit form of learning surpasses implicit learning in speed due to adults' heightened cognitive abilities. So perhaps for children, utilizing these implicit learning mechanisms paired with explicit systems (verbalized understanding and learning strategies) is the way to improve piano playing at a very young age. For adults, the key is to transfer explicit knowledge to implicit knowledge – studies focusing on immersion (exposure, practice, and motivation) have linked the success of second language adult learners to immersion. In comparing learning rate as a function of age, they compared learners immersed in second language vs. no immersion, eventually showing higher rates of accuracy among immersed learners. Adult learners progressed slowly but were still able to reach levels of proficiency. Studies show that adult learners utilized inhibition when learning a second language (Li et al. 2014) – Bilinguals rely on access to inhibitory controls for sounds, words, and grammar when utilizing the second language, displaying strong ability to tune out irrelevant information and attention switching (they performed better on the Stroop test - when words describing color are written in another color).

Music Perception

Basis of Music Perception:

Engaging in music creation is highly complex, involving various brain structures. The conscious perception of auditory, visual, and somatosensory stimuli relies on primary and secondary regions of the cerebral cortex, while other brain areas manage automatic facets of music-making. The prefrontal cortex (PFC) is involved in the creation, fulfillment, or deviation from expectations. Other essential areas are for motor control (motor cortex), tactile feedback (sensory cortex), auditory perception (auditory cortex), visual music reading (visual cortex), emotional expression (nucleus accumbens and amygdala), creativity, and memory (hippocampus). Structural differences in musicians' brains are evident in MRI data, showcasing larger volumes in specific regions.

Janzen and Thaut (2018) reiterate in their paper on cerebral organization how neuroimaging research has gone through great developments in the last 20 years, highlighting several subcortical and cortical areas involved in music processing, emphasizing the anatomical as well as functional connectivity between these regions – in particular, auditory-frontal networks, auditory-motor networks, and auditory-limbic networks. They move past "where" and "when" of task-related activity to understand how different brain networks work cross functionally to support cognitive, perceptual, and motor functions.

Incoming acoustic information is received by the outer and middle ear, which is then passed to the cochlea of the inner ear and converted into neural signals. The cochlea contains the basilar membrane, where properties are tonotopically organized based on sound frequency. This tonotopic representation means that neurons are systematically arranged topographically according to their sensitivity to various frequencies.

The basilar membrane is a crucial component of the cochlea in the inner ear that plays a fundamental role in hearing. It is a thin, flexible structure that runs along the length of the cochlea, separating two fluid-filled tubes (the scala tympani and scala media) within the cochlear canal. As sound waves enter the cochlea, they cause the basilar membrane to oscillate, and these movements vary along its length due to differences in its width and stiffness - narrower and stiffer at the base, becoming wider and more flexible toward the apex.

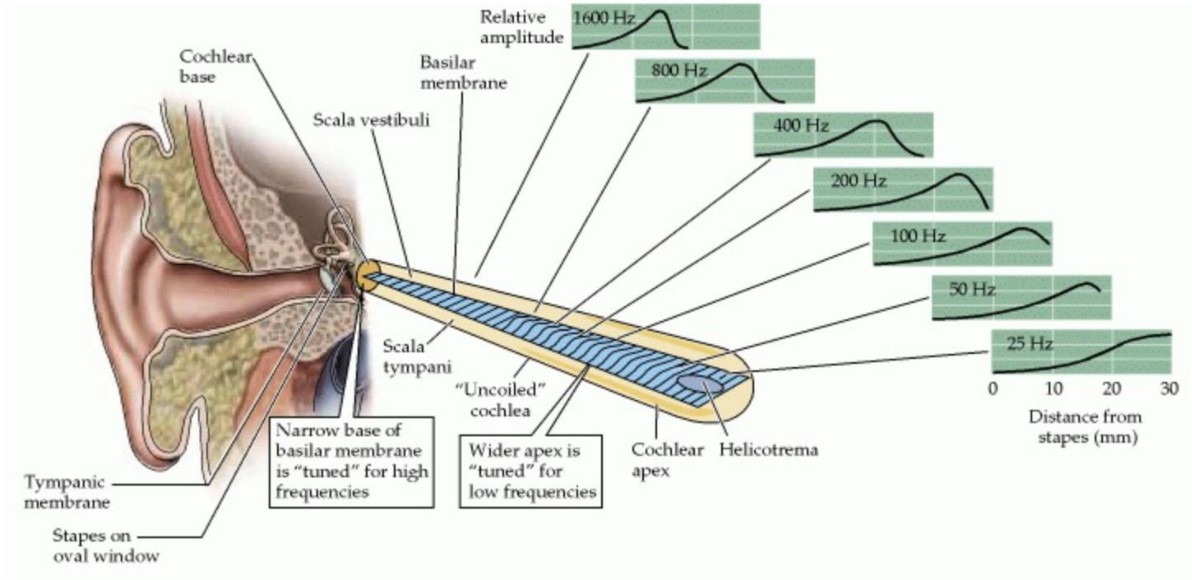
This physical variation allows the basilar membrane to be mechanically tuned to different frequencies of sound: higher frequencies cause more pronounced oscillations at the base, while lower frequencies peak towards the apex. This property underpins its tonotopic organization, where different frequencies of sound are encoded at specific places along the membrane. This encoding is critical for the translation of acoustic signals into neural signals, as the hair cells - sensory cells atop the basilar membrane – convert the mechanical energy of sound waves into electrical signals that the brain can interpret as sound. There are dendrites of spiral ganglion cells that synapse to hair cells on the basilar membrane. When the basilar membrane oscillates and triggers movement of the hair cells, the first neurons, the spiral ganglion, fire action potentials in the auditory pathway and transmit auditory signals.

The research discussed highlights a structured hierarchy in how we process music. The primary auditory cortex is essential for identifying single pitches and their variations within a melody (contour, intervals, chord discernment), while secondary auditory areas handle the task of discerning how these pitches relate to each other within a melodic line (relative positions).

More complex tasks, such as interpreting meaning, predominantly take place in non-auditory regions such as the frontal cortex.

Figure 10

Anatomy of the inner ear



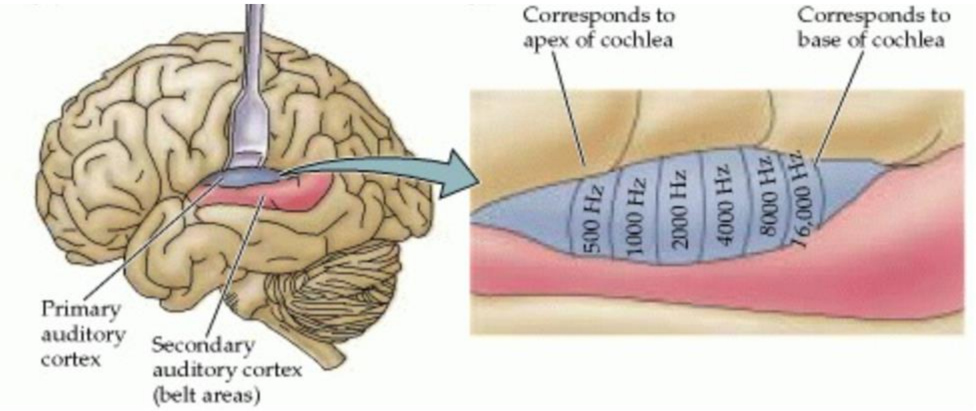
Note. From Neuroscience, by Purves et al., 2001

Specific brain areas are involved in the processing of musical structures. Regions like the inferior frontal gyrus and areas of the frontal cortex are highlighted for their role in interpreting expected or unexpected elements in music, such as harmonic and structural expectancies, syntax, as well as melodic and rhythmic deviations. This complex cortical network is essential for recognizing musical-structural irregularities and forming quick predictions about forthcoming musical events. Additionally, auditory processing is supported by two major neural pathways: the anterior-ventral pathway, focusing on the perception of auditory objects (the “what” aspects of sound), and the posterior-dorsal stream, which deals with understanding how sound moves and changes over time (the “how” and “where”). These pathways help in distinguishing and responding to changes in pitch and rhythm within a musical context, indicating a broader, fundamental role in general auditory processing.

Music perception involves primary and secondary auditory areas (A1, A2) and auditory association areas (AA) in the two temporal lobes. The primary auditory areas engage in basic auditory processing (pitch, loudness perception), time structures, and spectral decomposition of sound waves. The secondary auditory area surrounds the primary area, processing more complex features such as timbre. Located in the temporal lobe within Heschl's gyrus, A1 receives auditory information from the inner ear, traveling up the ascending auditory pathway. The A1 region analyzes basic auditory signals such as pitch, dynamic level, temporal structures, and spectral decomposition of sound waves. The A2 area is a belt surrounding the A1 region, processing more complex acoustical features such as timbre. Auditory association areas utilize what Altenmüller (2018) describes as "auditory gestalt principles", in which "pitch-time patterns" such as melody and words are processed (Wernicke's area).

Figure 11

Auditory cortex



Note. From Neuroscience, by Purves et al., 2001

Auditory processing is complex, as there is not only processing of acoustic structures, but also “patterns associations, emotions, and expectations”. Once these processes have been completed and synthesized, they contribute to the formation of memories and emotional associations, which are processed within the limbic system, including areas such as the ventral tegmental area (VTA) and nucleus accumbens (NAcc). This process commonly involves the hippocampus and dorsolateral prefrontal cortex (dlPFC).

Basis of Music Performance and Production:

The creation, formulation, or making of music involves voluntary and skilled motor movements. Voluntary skilled movements involve several cortical regions in both hemispheres: the primary motor area (M1), the supplementary motor area (SMA), the premotor area (PMA), and the cingulate motor area (CMA). The SMA, PMA, and the CMA are known as secondary motor areas because they are involved in processing movement patterns rather than simple movements. Subcortical structures such as the basal ganglia and the cerebellum are also integral to the motor system, as well as the primary somatosensory area (S1) in the parietal lobe. The parietal lobe is also important because much of the processing done in many sensory regions converge there. In the posterior parietal area, the body's position and coordinates in space or tracked, and visual information is passed on to these coordinates, which aids during musical tasks such as sight-reading music.

The primary motor area, M1, is located in front of the central sulcus, in the precentral gyrus. The M1 represents the movements of different body in a somatotopic or homuncular fashion. The control of certain movements requires more nerve fibers, certain parts of this homuncular ordering have greater density due to the activations of these body parts that require more attention. This is why the hands, lips, and tongue require almost two-thirds of the neurons in this area (Roland & Zilles, 1996, as cited in Altenmüller et al., 2018). Altenmüller et al. (2018) further elaborates that:

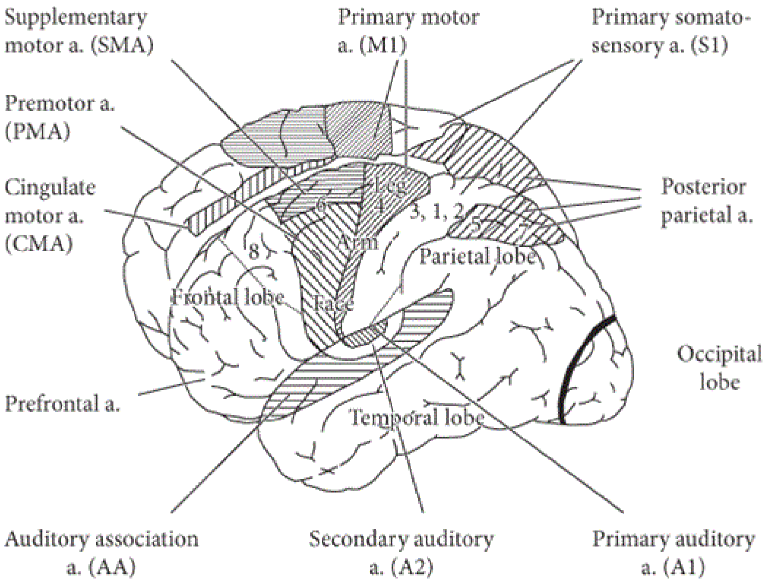
> The primary motor area does not simply represent individual muscles; multiple muscular representations are arranged in a complex way so as to allow the execution of simple types of movements rather than the activation of a specific muscle. This process is a consequence of the fact that a two-dimensional array of neurons in M1 has to code for

three-dimensional movements in space (Gentner & Classen, 2006, as cited in Altenmüller et al., 2018). Put more simply, our brain does not represent muscles but rather movements".

There have also been studies done on mirror neuron networks, in which trained pianists would observe another pianist's hand movements. When observing, it was found that that additional areas in the primary motor cortex, secondary auditory cortices, and temporal lobe, premotor, and parietal cortex were also activated (Altenmüller, 2022) – this points to instrumental demonstration as a powerful teaching tool.

Figure 12

Auditory and motor areas



Note. From "Brain changes associated with acquisition of musical expertise" by Altenmüller, 2022)

The SMA (supplementary motor area), CMA (cingulate motor area), and the PMA (premotor area) are all secondary motor areas, in which these regions are processing motor patterns rather than simplistic motor actions. As well, there are subcortical regions involved in motor movements, such as the basal ganglia and cerebellum. Additionally, located in the parietal lobe is the primary somatosensory area (S1), responsible for processing various sensory information.

Located anterior to the primary motor area and medial side of the cortex, the SMA is engaged for sequencing motor movements internally stored in memory and is also engaged when sequential movements are made based upon memorized cues. Because it has internally stored segments at a time and has made a hierarchy of sequential movements, the SMA is also important for pitch and rhythm. It is engaged also when either performing or even visualizing or imaging music. The premotor area (PMA) is involved in reacting to external stimuli like sounds or sights. It anticipates, plans, and prepares movement patterns in response to visual or auditory cues, and is heavily utilized in learning, executing, and recognizing limb movements. The CMA is located in the medial portion of the cortex as well, but its engagement is still uncertain.

The basal ganglia, deeply seated within the brain as a subcortical structure, plays a crucial role in voluntary motor movements. The cortical and subcortical areas are interconnected via the thalamus, which connects the basal ganglia, located deep inside the brain, to the motor and sensory cortices. The components of the basal ganglia are critical in the organization and sequencing of collective movements, especially in automaticity – sequencing movements (such as finger movements) until they are automatic, comparing the goal of motor movements to previously experienced movements. Ericsson (2018) expands on the basal ganglia, clarifying the cortex and limbic emotional systems, specifically the amygdala and the nucleus accumbens, converge.   So the basal ganglia is involved in processing motor behaviors and the emotional meaning in terms of reward. Additionally, the cerebellum is involved in timing, accuracy, and error correction when learning new skills. The cerebellum, parietal, and motor cortex are said to be part of the encoding process of internal models of motor movements. Altenmüller and colleagues describes this “internal model”, meaning the neural process that “simulates the response of the motor system in order to estimate the outcome of a motor command”. The cerebellum is known as a universal control system that contributes to learning, and to optimizing a range of functions across the brain (Ramnani, 2014, as cited in Altenmüller et al., 2018).

The cerebellum is a multifaceted brain region, playing a pivotal role in movement optimization and error correction. It is highly engaged when it comes to skill acquisition, fine-tuning the precision and timing of movements. It is thought to be part of a network involving the parietal and motor cortex that encodes internal models of these newly acquired skills. With extensive connections to nearly all brain regions, particularly those linked to memory and higher cognitive functions, the cerebellum acts as a universal control system. In this sense, the cerebellum plays a crucial role in contributing to the learning and optimization of brain networks (Ramnani 2014, as cited in Brown, 2015).

The cerebellum perhaps receives this specialty as a control area because it has the most neurons packed into a structure that is only one-tenth the size of the rest of the brain. Comprised of a high density of cells, this structure is also composed of neurons arranged into local circuits that are identical to one another, in comparison to the cerebral cortex that has various cell types in different organizations – “Cerebellar regions are differentiated only by the cortical areas to which they connect – medial regions to sensory and motor cortices, and lateral regions to the frontal, parietal, and temporal lobes” (Brown, 2015, p.59). When listening, performing, and imaging music, the cerebellum receives both sensory and motor information. Because the cerebellum has dual processing capabilities, this structure has the ability to compare repetitions.

These repetitive iterations lead to optimizing the motor movement, as well as creating an internal model of the commands before the movement is executed as well as the sensory consequences that ensue following movement. Brown further elaborates the formation of internal models serves as the foundation for learning and enables the identification and correction of movement errors. This internalization and pre-play before movement execution strikes a similarity to hippocampal memory formations discussed in a later chapter. Support for this interpretation of cerebellar function is derived from research involving individuals acquiring new skills - for example, there is shown to be greater activity in the cerebellum when pianists were playing more complex rhythms in comparison to non-musicians, but the reasoning could be because there is greater cross-network functioning between the frontal cortex that deal with working memory (Brown, 2015).

In terms of motor skill execution, “the complexity and precision of expert movement may be enabled in part by greater independence and economy of individual limb movements. For instance, expert pianists are capable of controlling their hands and individual fingers more independently of one another than less-skilled pianists... in addition, expert pianists organize their upper-limb movements during performance such that they minimize muscle effort relative to less-skilled pianists.” Feedback monitoring also occurs in which “performers receive visual, tactile, proprioceptive, and sometimes vestibular feedback during performance, in addition to the auditory feedback (Gabrielsson 2003, as cited in Brown 2015).

Neural Networks, Neuroplasticity, and Musical Training:

Music serves as a great model for studying any changes that happen over time with brain function and brain structure when expertise is gained. These changes that happen over time are referred to as brain plasticity. There is high demand on the nervous system when performing music, and the performer also experiences a "rich multisensory and motor experience". Altenmüller et al. (2018) couldn't put it into better words:

> A pianist, for example, must draw on a whole set of complex skills, including translating visual analysis of musical notation into motor actions, coordinating multisensory information with bimanual motor activity, developing fine motor skills in both hands coupled with metric precision, and monitoring auditory feedback to fine-tune a performance as it progresses (Altenmüller et al., 2018, p. 1480).

The authors further elaborate:

> With respect to mechanisms and microstructural effects of plasticity, our understanding of the molecular and cellular processes underlying these adaptations is far from complete. Brain plasticity may occur on different time scales. For example, the efficiency and size of synapses may be modified in a time window of seconds to minutes, while the growth of new synapses and dendrites may require hours to days. An increase in gray matter density, which mainly reflects an enlargement of neurons due to increased metabolism, needs at least several weeks. White matter density also increases as a consequence of musical training. This effect is primarily due to an enlargement of myelin cells which wrap around the nerve fibers (axons) and dendrites, greatly contributing to the velocity of the electrical impulses traveling along them (Altenmüller et al., 2018, p. 1488).

Neural network connectivity:

Frontal cortex activity is linked to both cognitive demands and the demands of specific tasks (Jancke & Thaut 2018). When there are tasks involving maintaining or rehearsing musical information, the working memory network is activated which includes the ventrolateral and dorsal premotor cortices, planum temporale, inferior parietal lobe, anterior insula, and subcortical structures. Additionally, the medial prefrontal cortex is heavily involved in tasks that demand self-referential judgments, musical semantic memory, and autobiographical aspects. The activation of these areas varies according to the attentional demands of different tasks, suggesting a complex interaction between cognitive functions and neural mechanisms in the processing of musical information. This reverts to the neural oscillations section within this paper, in which understanding functional connectivity within the brain is helpful in interpreting which areas will "speak" to one another during complex musical tasks.

Research demonstrates a coupling between the auditory and motor systems in the brain, illustrating that even mental imagery of sounds can evoke neural representations of the physical actions needed to produce those sounds (Jäncke & Thaut, 2018). Involuntary musical imagery, where music spontaneously plays in one's mind, involves the frontal and temporal cortices, the anterior cingulate, and the left angular gyrus. Voluntary musical imagery, which involves the conscious generation of mental musical representations without the perception of sound, activates areas including the secondary auditory cortices, parietal cortex, inferior frontal regions, and motor areas like the supplementary motor area (SMA) and pre-SMA. Further studies reveal that motor areas are activated not just when musicians engage with familiar music, but also when non-musicians listen to music they have learned to play, indicating a robust linkage between auditory perception and motor action within human cognition. This touches upon an interesting area in which a mere aural representation or perception of sound can induce a neural representation of the movement as well required to create that particular sound. This is evidence supporting theories stating coupling within perception and action areas in the brain.

A substantial amount of neuroimaging research has underscored the interplay between auditory and motor cortices (Koshimori &Thaut, 2018; Jäncke & Thaut, 2018). Studies indicate that both listening to, and mentally rehearsing auditory rhythms boost the connectivity between these brain regions. Musical training further intensifies this integration. Additionally, evidence shows that engaging with music featuring a pronounced beat enhances motor pathway activity from the primary motor cortex to the spinal cord (corticospinal), highlighting how even passive listening can activate these motor circuits. Research using transcranial magnetic stimulation aligns with this finding, demonstrating that timing the stimulation to music increases motor excitation in muscles used in rhythmic movements like foot tapping, particularly among trained musicians. Overall, these studies demonstrate the significant functional and anatomical connections between auditory and motor regions, which are essential for auditory perception, generating predictions, and synchronizing movements to music.

Temporal perception and the execution of timed actions rely on the interaction of multiple brain areas, including the cerebellum, basal ganglia, thalamus, SMA, pre-SMA, PMC, and auditory cortex. These areas form complex networks essential for sensorimotor synchronization and temporal processing. Emerging research identifies at least two primary networks involved in timing: the cerebellum's role in sensory prediction errors, motor adaptation, and duration-based timing; the other, the basal ganglia and SMA's influence on timing and rhythmic movements.

Research increasingly shows that cortico-cerebellar networks are primarily active during movement synchronization to external cues, whereas they are less engaged during self-initiated or internal motor behaviors. This supports the understanding of the cerebellum's function in merging sensory and motor inputs, fundamental sensory prediction for motor timing, and adjustment during sensorimotor synchronization. Similarly, the premotor cortex is implicated in managing movements influenced by external sensory signals, with a specific role in predicting motor timing and temporal adjustments, as well as in coordinating the timing of sounds to corresponding motor actions.

Recent research has highlighted the involvement of a distributed network encompassing the basal ganglia, thalamus, and cortical areas like the SMA, pre-SMA, premotor cortex, and auditory cortex in beat perception. The basal ganglia, particularly the putamen, are crucial for predicting upcoming events based on relative timing mechanisms. This network is also associated with reward prediction, associative learning, and harmonic processing (Jäncke & Thaut, 2018). Studies have shown that functional connectivity between the basal ganglia, cortical motor areas, and the auditory cortex increases significantly during rhythm perception, indicating their importance in representing pulse and rhythm even without movement cues. Moreover, the basal ganglia and SMA are key in maintaining internal representations of beat intervals during sensorimotor tasks, especially in the absence of external cues. Dopamine receptors play a vital role in mediating the processing of temporal information within the basal ganglia-thalamo-cortical circuit. Overall, the cortico-cerebellar and basal ganglia-thalamo-cortical networks work together in temporal perception and motor timing, with future studies aiming to elucidate their interactions in both motor and non-motor functions.

The limbic and auditory systems are intricately connected, forming an important network for the emotional processing of auditory information. Key pathways include direct and indirect connections between the auditory system and areas like the amygdala, which receives signals from the temporal cortex and primary auditory cortex, as well as the thalamus. This network allows for quick responses to simple, intense sounds via a subcortical route and more complex emotional interpretations through a slower, cortical path. Neuroimaging studies have demonstrated that various limbic regions, including the amygdala and hippocampus, are activated by music, influencing emotional responses and memory processes related to music-evoked emotions. Additionally, the ventral striatum, including the nucleus accumbens, plays a key role in the pleasure and reward experiences derived from music, facilitated by dopamine release in these areas. Overall, these findings highlight the complex interplay between auditory and limbic systems in emotional sound processing and the broader implications for our understanding of neural responses to music and sounds.

These studies using EEG have indicated that listening to music leads to reconfiguration of brain functional networks. Research indicates that music listening enhances interregional synchronization within the brain, suggesting that music processing involves coordinated activity across various cortical and subcortical areas. This coordination demonstrates the significant impact of music on the brain's functional organization. This comprehensive analysis underscores the complexity of neural networks in music processing and sets the groundwork for future research into how these networks dynamically organize during music listening. These studies also support the neurobiological mechanisms outlined earlier in this paper.

Neuroplasticity and Musical Training:

Altenmüller et al. (2018) presents four compelling reasons why brain plasticity is particularly pronounced in music performance compared to other skilled activities. First, the intensity of goal-directed training in music is notably high. Second, the commencement of musical training for professional musicians typically occurs at a very young age, aligning with heightened central nervous system adaptations. Third, musical engagement is intertwined with heightened arousal and positive emotions, although it also entails stressors that trigger changes in hormonal activity, including adrenaline for arousal, endorphins for joy, dopamine for rewarding experiences, and stress hormones due to fear of failure, all contributing to neuroplastic changes. Lastly, public performances stimulate the release of social hormones like oxytocin and serotonin, further facilitating plastic adaptations. However, we need to exercise caution when suggesting that adaptations are more prevalent in music compared to other activities, as the observed differences could be attributed to the uniformity of the sample being studied.

Musical training also induces significant changes in both the auditory and motor systems mentioned above, leading to enhanced brainstem representation of musical sounds and stronger cortical responses (Brown, 2015). Specific adaptations occur in the somatosensory/motor system based on the specific instrument performed by the subject. Anatomical changes in auditory and motor regions, including white-matter pathways, are linked to musical training. Longitudinal studies with children demonstrate causal connections between musical training and both structural and functional changes. Additionally, there is evidence of enhanced interactions between auditory and motor systems in musicians, such as coactivation of auditory and premotor cortices during music performance. The relationship between training and auditory-motor integration is evident in enhanced premotor recruitment after specific training. These findings underscore the intricate connections between musical training, neural organization, and the integration of auditory and motor systems.

Figure 13

Sound and action linked by premotor and auditory regions

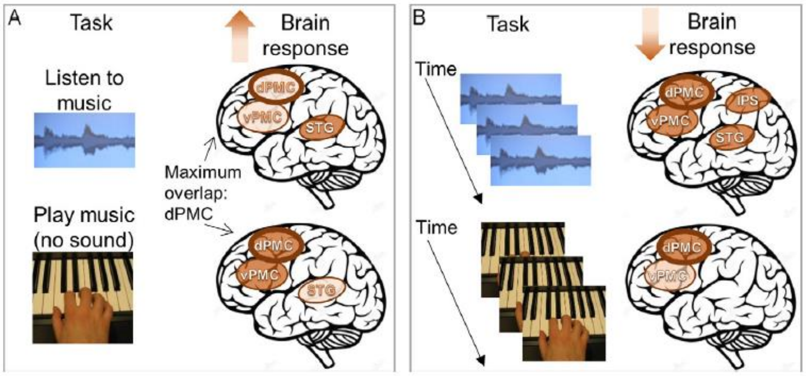


FIGURE 2

Perception and production of music in musicians. (A) Musicians engage premotor and auditory cortex when either listening to music without performing (top panel) or performing music silently (bottom panel), suggesting that premotor and auditory regions link sound with action (Bangert et al., 2006; Baumann et al., 2007). (B) Musicians also demonstrate adaptation or decreased response in premotor cortex to both repeated listening and repeated performance of music (Brown et al., 2013), further supporting a role for premotor cortex in integrating sound and action. dPMC, dorsal premotor cortex; STG, superior temporal gyrus; vPMC, ventral premotor cortex; IPS, intraparietal sulcus.

Note. From “Expert music performance: cognitive, neural and developmental bases” by R. Brown (2015).

Several studies have found enlargement of the corpus callosum in musicians in comparison to a non-musician control group, which was due to an “increase in myelination in the crossing fibers of the hand areas of both hemispheres”, related to the demands of bimanual coordination. In other DTI (diffusion tensor imaging) studies, there are also several white matter tracts that increased due to piano training in childhood:

> A relatively new technique that can be used to study differences in fiber tract volume and direction is diffusion tensor imaging (DTI). This provides information about white matter micro-structures by measuring diffusion properties of water molecules that move preferentially along the myelin sheets of axons. The degree of diffusivity is quantified as fractional anisotropy (FA), a measure allowing the assessment of orientation and direction of axons and their degree of myelination" (Bandettini 2009, as cited in Brown et al., 2015).

Extensive and consistent practice over many years leads to significant changes in brain structure induced by music training. While the belief that practice alone results in expertise is not entirely accurate, long-term practice is strongly associated with expertise across various fields. Research consistently finds that the length of training correlates with both brain structural differences and task performance. Studies in animals also support the impact of practice on brain organization, showing increased representations in motor areas, alterations in gray and white matter, and boosts in synapses and dendritic spines. These neuronal changes encompass neurogenesis, synaptogenesis, modifications in neuronal shape, as well as enhancements in axon number, size, fiber density, and myelination in white matter (Zatorre, 2005).

Music training drives brain plasticity effectively due to its highly specific nature of practice. Musicians, often focused on a single instrument, repeat precise movements and listen attentively to associated sounds, engaging in a cycle of prediction, feedback, and error correction during practice. Auditory-motor prediction is central to this process, supported by brain imaging studies showing increased premotor cortex activity when listening to learned melodies. Feedback and error correction led to functional and structural brain changes driven by decreased error and improved precision. This is called error-driven learning, and during phases of high development plasticity this type of learning can be the reason for structural changes in the brain found in adult musicians. A second factor highlighted by Penhune (2019) regarding why music training stimulates brain plasticity is the multisensory nature of music making. This involves integrating auditory, visual, somatosensory, and proprioceptive information, as sounds are associated with actions. Training operates on a feedback-to-error-correction cycle, utilizing all senses to produce the desired output.

A final reason why music training promotes plasticity is its rewarding nature. When musicians strive to master a piece, they imagine its desired outcome, form a motor plan, and use both as benchmarks for their performance. Errors in execution lead to corrections and learning, while accurate performance is rewarding. Humans show a strong drive to practice and refine various skills, and Penhune (2019) describe three aspects of reward: the act practice itself may be inherently rewarding, the intrinsic satisfaction of performing well, and the pleasure derived from accurate performance during practice. The intrinsic pleasure of music is believed to be linked to dopamine-modulated predictive systems that regulate reward in various domains, including drugs, food, and money (as mentioned previously concerning dopamine as a neuromodulator). Therefore, if playing a musical piece triggers dopamine release, it would enhance the learning process.

Altenmüller and Furuya (2018) discuss the age at which one begins practice, the quantity and quality of practice, genetic predisposition, and accompanying factors like stress or muscular strain dictate the quality and type (adaptive or maladaptive) of brain changes. Additionally, the optimal periods for brain development, or "sensitive periods” (critical periods) appear influenced by both genetic factors and differ across various sensory, motor, and cognitive functions. Altenmüller et al.’s concept of “metaplasticity” is argued, introducing a “scaffold metaphor”, suggesting that early musical training stabilizes the sensory-motor system and offers neuroprotective benefits against focal dystonia development. The authors state, “these not only enhance musical skill acquisition and guard against disorders triggered by extensive training, but also serve as ingredients for better shaping lifelong neuronal development” (Altenmüller and Furuya, 2018, p. 550).

Research on how musical training affects brain development in children suggests that early involvement in music can lead to differences in brain structure and function, appearing as soon as a few months to two years into training (Putkinen et al., 2018). Both cross-sectional and longitudinal studies show that these differences are not only observable but also significant in contributing to cognitive skills relevant to academic success and overall well-being. Early studies recorded stronger brain responses to music and instrument-specific sounds in children engaged in music lessons compared to those not involved in music. Further research has confirmed these findings, demonstrating that musical training enhances brain responses to both music and speech, suggesting a broader impact on auditory processing capabilities. These studies collectively highlight the potential of musical training to influence brain development positively and imply a causal relationship between structured musical practice and enhanced neural function in children.

Research indicates that musical training in children enhances their ability to detect changes in sound, as shown by studies measuring Mismatch Negativity (MMN) – this is similar to phonetic discrimination in language described by Kuhl (2010). Initial cross-sectional studies found improved neural response to musical changes in trained children. Subsequent longitudinal studies, comparing children with musical training to those without, revealed that training from an early age integrated into school curricula can significantly increase MMN responses to various musical elements over time (Putkinen et al., 2014). For example, children exposed to structured music education showed greater neural enhancements in processing changes in melody, rhythm, and chords compared to their untrained peers. Further studies, including those assigning children to music versus non-musical activities like painting (Alain et al., 2019), consistently show that musical training sharpens auditory processing and possibly extends to better language processing skills, suggesting broader cognitive benefits from early musical education.

Over the past couple decades, numerous experiments have demonstrated that music training induces structural alterations in the brain, particularly within the auditory-motor network. According to Penhune (2019), these structural disparities between musicians and non-musicians can be attributed to four factors. Firstly, inherent predispositions or existing brain architecture may predispose individuals to excel in music training. Secondly, prolonged training leads to structural modifications in the brain. Thirdly, specific developmental periods may facilitate brain changes that are not as readily achievable later in life. Lastly, the rewarding aspects of music serve to enhance brain plasticity further.

Cross-sectional studies have revealed structural differences in both white and gray matter between adult musicians with extensive training and adult non-musicians with limited or no musical experience. A consistent finding across these studies is the enhancement of the primary auditory cortex, including Heschl's gyrus, characterized by increased gray matter volume and cortical thickness in this region. Additionally, enhancements in gray matter are often observed in motor-related areas, such as the primary motor cortex, pre-motor cortex, parietal regions, cerebellum, and basal ganglia. Differences in white matter tracts, notably in the corpus callosum, have also been noted. Furthermore, other regions that showed differences between musicians and non-musicians were the frontal and parietal cortex, areas that overlap in both music and language production, especially with working memory.

The effects of musical training in childhood are largely studied due to the fact that sensorimotor activity especially during early critical periods of childhood development (as mentioned above under Critical Learning) can have lasting impacts on long-term brain plasticity. Penhune (2019) mentions the first longitudinal study examining children 15 months after piano training in 6 to 8 year olds by Hyde and colleagues in 2009 – researchers discovered an increase in gray matter volume in auditory, motor cortex, and corpus callosum. A subsequent study conducted by Habibi et al. (2017) demonstrated comparable findings, indicating increased white matter in the corpus callosum among the same age group over a two-year period. Of particular interest is the similarity in areas of change observed following long-term musical training in adults, including alterations in the auditory cortex, motor cortex, and corpus callosum.

The differences in brain structure between musicians and non-musicians are not solely attributed to intensive training but are likely influenced by a combination of training-induced changes and pre-existing individual differences (referring to pre-existing anatomy capable of facilitating the acquisition of new musical skills) in the brain that predispose some individuals to engage in music (Penhune, 2019). Evidence suggests that certain brain features, such as gray matter concentrations in auditory regions and white matter tracts connecting auditory and motor regions, correlate with musical abilities and response to training. Studies on twins have also been conducted to assess the relative importance of genetics versus training. "They found that the twins who played had greater cortical thickness in auditory and motor regions as well as white matter enhancements in the corpus callosum compared to those who did not" (de Manzano &

Ullén, 2018). These findings offer the most compelling evidence to date supporting the causal impact of music training on brain structure, as opposed to predisposition.

Research showing that genetic factors can influence musical ability suggests that the benefits seen in musicians aren't solely due to the theory of deliberate practice as well, as previously thought (Ericsson et al., 1993). While genetic predispositions and experience-induced brain changes can coexist, it's important to acknowledge that genetics play a role in the perceptual, motivational, and cognitive skills related to music, which helps explain differences between musicians and non-musicians. Studies with twins investigated how genetic and environmental factors affected music perception (melodic detection and rhythmic perception) – the authors' results (Ullén et al., 2016) suggest that how much genetic or environmental factors affect music perception depends on the task in question – whether it is based more on formal vs. implicit knowledge.

The current research on brain structure in musicians suggests that certain structural features in the auditory-motor network may predispose individuals to pursue music training. The effects of training depend on factors like age of start and the interaction with the maturation of brain regions and connections. Early training during specific phases of development may lead to a scaffold or metaplasticity effect, where this metaplasticity effect is where experience (in this context the musical training) shapes the brain's potential for plasticity in the future, potentially influencing how regions respond to future experiences. Studies show that musicians exhibit enhanced learning of sensory and motor skills, suggesting a role for metaplastic effects in music training. Additionally, aptitude for music training may depend not only on auditory or motor skills but also on genetic factors influencing propensity to practice and personality traits like openness to experience, which are associated with long-term engagement in music. Therefore, becoming a successful musician requires both inherent talent and the right personality characteristics to sustain rigorous training and embrace challenges.

In many of these studies that relate plasticity to musical training, Penhune (2019) mentions there are certain confounds that appear, such as the starting age of music training which may be confounded with years of musical training. To combat this, researchers have found ways to conduct experiments in which they used early training (before age 7) vs. late training (after age 7) subjects – they would match ET and LT groups on important potential confounds that included years of music experience, amount of formal training, and current practice hours. Findings suggest that early music training during the developmental period of peak maturation in motor regions and the corpus callosum could enhance brain plasticity. This interpretation implies a scaffold effect, where early training sets the stage for continued or increased brain plasticity through later practice (Steele & Zatorre, 2018). In summary, recent research challenges the straightforward notion that early music training uniformly enlarges brain structures like the primary motor cortex and corpus callosum. A study examining cerebellar volumes in musicians found that early-trained musicians had smaller volumes in specific cerebellar lobules compared to late-trained musicians. This contradicts previous findings and suggests that the cerebellum's unique developmental timeline and uniform structure may play a role in how early experience affects brain plasticity. The suggestion here is that as cortical areas expand due to training, there might be a corresponding decrease in cerebellar expansion, hinting at a possible inverse connection between changes in the cortex and the cerebellum with training.

Penhune (2019) proposes avenues for future research in musical training. First, researchers should consider participant characteristics such as training age or age of onset. Secondly, studies should involve larger sample sizes and employ multiple imaging techniques, moving beyond focusing solely on individual brain regions to examine changes at the network level.

Putkinen et al. (2018) also discuss executive functions: Executive functions are top-down mechanisms for cognitive processes that control behavior. They include selective attention, working memory, cognitive flexibility or set-shifting, and inhibition. They support planning, decision making, behavior recognition, and performance monitoring (higher order functions), integral aspects of playing a musical instrument. Therefore, it is reasonable to assume that higher executive function leads to better musical training, or that musical training positively affects executive function.   Studies have supported this, showing that adults and children with musical training were outperforming those untrained counterparts in terms of working memory, set-shifting, and inhibition – other further experiments using fMRI data revealed that there was a stronger recruitment of prefrontal and subcortical regions than non-musicians, which is perhaps part of the neural reasoning for the outperformance.

Research suggests that musicians may have better domain-general executive functions, but findings are inconsistent about which specific functions are improved and not all studies confirm that musical training enhances these cognitive abilities. Additionally, many of these studies are correlational and cannot clearly attribute differences between musicians and non-musicians to the effects of training alone. Recent critical analyses and meta-analyses argue that the evidence supporting the transfer of musical training to improvements in working memory and other cognitive areas is weak and problematic. This skepticism extends to the broader concept of far transfer, questioning the idea that skills developed in one area can broadly improve unrelated cognitive domains.

Loui et al. (2018) discusses the effects of musical training on executive functions, how these findings relate to far-transfer (every day activities), and the specifical neural mechanisms involved in executive function and transfer. Loui (2018) states,

> Unlike passive listening, long-term music training engages more of our neural and cognitive circuitry and thus can be expected to induce structural and functional plastic changes in the brain. The importance of discerning whether musical training promotes any advantages to EFs relates to the question of the transferring of skills, or transfer. The transfer and generalization of learning and skills from one area to another, then, can increase general cognitive capacities. Near transfer occurs within a specific modality (e.g., music and speech) whereas far transfer occurs between two less obviously related domains (e.g., music and IQ or music and conflict monitoring). While nearer forms of transfer between music and related areas have been demonstrated, far transfer is harder to prove (Loui et al., 2018, p. 270).

To explore the impact of music on executive functions and cognitive abilities, researchers have conducted association studies to investigate potential near transfer effects. Typically, these studies involve two groups: one with musical training and the other without. Research discussed in Loui's paper (Patel, 2011, as cited in Loui, 2018) suggests that musical training can enhance speech processing and encoding through attention signaling. Musical training is recognized for its ability to refine auditory skills like pitch discrimination, which has been linked to improved reading and phonemic awareness. Furthermore, Patel's Shared Syntactic Resource Integration Hypothesis (SSRIH) proposes that syntax processing in both music and language relies on overlapping brain regions, implying that musical training could fortify language comprehension through cognitive control mechanisms. Studies indicate that these shared cognitive processes can lead to enhancements in tasks involving syntactic structures and executive functions, suggesting that musical proficiency might influence broader cognitive domains extending beyond music and language. This aligns closely with findings from the salient attention stimuli study discussed in an earlier

Proving far transfer, or the idea that skills learned in music can benefit areas beyond music, is challenging less reliable – when comparing musicians to non-musicians, there are confounding factors that can't be controlled such as parental education, socio-economic status, or home environment variables outside of the experimenter's ability to control. Longitudinal studies attempt to eliminate these confounding variables, and randomized controlled trials are considered the most rigorous method. Other longitudinal behavioral and ERP studies have compared music training with sports or visual arts, longitudinal studies with randomized control groups provide the most significant evidence of the far transfer effects of music to other domains.

Loui et al. (2018) compares executive function vs creativity as the executive functions work with "conflicting constraints", while creativity is "relatively unconstrained thought processes…these mental processes involve selective attention and stream segregation, long-term and autobiographical as well as working memory, idea generation and evaluation, and expectation and prediction, as well as the ability to switch between these processes". In other words, creativity encompasses executive functions, such as attention, working memory, flexibility, etc.

Peak and Expert Performance:

"Narrowly defined, mental training is understood as the vivid imagination of movement sequences without physically performing them. As with observation of actions, principally the same brain regions are active as if the imagined action is performed; that is, the primary motor cortex, the supplementary motor cortex, and the cerebellum" (Kuhtz-Buschbeck et al., 2003).

The professional level of music making is highly demanding. It involves complex movements that must be coordinated with auditory, somatosensory, and visual cues and feedback. Moreover, musicians require the retrieval of musical, motor, and multisensory data from short-term and long-term memory, while also engaging in continuous planning with working memory. Furthermore, they must anticipate, monitor, and promptly adjust the consequences of their motor actions in real-time.

A highly influential study on practice was completed by Ericsson, Krampe & Tesch-Romer in 1993 at the Berlin Academy of Music. Deliberate practice, as emphasized by Ericsson and colleagues, is essential for developing complex skills and achieving excellence in music. This form of practice involves goal-oriented, structured, and effortful sessions coupled with motivation and focused attention. Ericsson's study on musicians at the Berlin Academy of Music highlights the importance of both the quantity and quality of practice in distinguishing between professional and amateur musicians. Skilled musicians dedicate considerable effort and concentration to their practice, actively planning, imagining, monitoring, and adjusting their playing. They also seek support from peers, including family and friends, in their pursuit of mastery. Their argument was that the greatest distinction between professional and amateurs, and successful or less successful learners, was the amount of deliberate practice taken over the years.

The concept of deliberate practice has also been refined to encompass "sensitive or critical periods", in which specific sensory motor skills such as finger independence are developed and matured in the CNS. However, as previously mentioned, the notion of deliberate practice being the sole factor of expertise has been recently challenged – "The issue of nature, vs. nurture, or genetic predisposition vs. environmental influences and training in musical skills is complex, since the success of training is itself subject to genetic variability" (Ericsson, 2018). Aspects under the umbrella of goal-directed "deliberate practice" are self-monitoring, anticipation of the consequences of one's actions, motivation, and focused attention, which involve great diversity in its neural networks, particularly the nucleus accumbens and memory structures such as the hippocampus. Sensory-motor skills show activity in premotor, motor, and parietal cortical areas as well as in subcortical brain structures such as the basal ganglia and the cerebellum. Brain plasticity may change due to strengthening, quieting, or growth of synaptic connections, or increase in myelination, increasing the speed of electrical impulses.

In the exploration of musical expertise and maintenance, the section "Methods for Studying the Acquisition and Maintenance of Expertise" from Cambridge Handbook on Expert Performance (Ericsson, 2018), the authors categorized the primary methods collected from studies into: Diaries/Training Logs, Systematic Observation (observing performers in their practice environments), experimental approaches, and retrospective approaches (reflects on their past experiences, behaviors, and characteristics). The retrospective approach to collecting and assessing practice history information offers an alternative option to longitudinal studies. The retrospective approach includes questionnaires, qualitative interviews, and longitudinal and prospective follow-up. However, qualitative results prove to be problematic, with authors stating "although qualitative interviews generate large amounts of detailed information, this approach is particularly labor intensive and time consuming. As a result, sample sizes are typically small, and often homogeneous. Therefore, the generalizability of findings beyond the respondent sample may be limited. Moreover, despite rigorous methods typically involved in thematic analysis of data, there is ultimately a degree of subjectivity that also impacts the generalizability, reproducibility, and validity of the findings. These methods might work best when used in combination with quantitative methods, or for exploration of new ideas and areas relevant to skill development."

Numerous studies have illuminated the direct correlation between the duration of practice and deliberate practice with proficiency levels and overall performance. Furthermore, Ericsson, referencing Williamon's book from 2004, emphasizes that elevating the quality of practice demands considerable exertion and the cultivation of metacognitive skills. Building upon this, Chaffin et al.'s 2003 study delves into the intricate practice methods of a solitary classical musician. The process begins by grasping the "big picture" through sight-reading, analysis, or immersion in recordings, thereby crafting an aural representation of the entire piece. Then, technical refinement is undertaken in segmented sections, followed by the integration of the entire piece, smoothing transitions between sections. This approach facilitates the transformation of memory from explicit to implicit, aided by the construction of an internal roadmap to navigate potential memory lapses. As the performer progresses, attention shifts towards refining nuances, solidifying tempi, and simulating a live performance for an audience. Finally, there is the maintenance phase, which can be a lengthy span of time.

In Ericsson (2018), the authors explain that Fitts and Posner (1967) established a model that describes skill acquisition as a progression from cognitive engagement to autonomous execution. Initially, individuals grapple with the cognitive aspects of a task, gradually transitioning to associative processes, and ultimately achieving autonomous proficiency. This signifies a diminishing need for cognitive mediation as competency improves. On the other hand, novices tend to concentrate on “technical, low-level aspects”, whereas experts direct their attention towards higher-order issues, like “strategic or aesthetic nuances.” This shift in focus shows the refinement of expertise, which encompasses not only skill execution but also the ability to navigate complex task constraints within a domain. The authors reiterate that "altogether, the development of expert performance can be seen as an adaptation to the typical task constraints of the domain, involving changes in cognitive, physiological, and perceptual-motor parameters that facilitate superior performance”. In essence, expertise emerges as a multifaceted adaptation to the demands inherent in a given domain, reflecting the integration of cognitive, physical, and perceptual faculties to achieve superior performance.

Achieving expertise in music demands the orchestrated involvement of various systems responsible for sequencing pitch and temporal events. As previously mentioned, key motor regions, including the basal ganglia, cerebellum, and supplementary motor area (Brown, 2015), are integral to movement control, optimization, and learning. The SMA is essential for planning sequential segments during performance, akin to "chunking" music segments. Expert musicians may show heightened engagement of SMA regions, but there's also evidence of reduced activity in auditory and motor areas during simpler tasks, indicating increased network efficiency (Brown, 2015). While the basal ganglia's role in timing tasks is well-established, its involvement in processing pitch sequences remains less explored, highlighting an area for further investigation in understanding the intricate process of music processing.

Altenmüller et al. (2022) emphasizes that practice primarily involves procedural knowledge, learned through experience. The authors state,

> Performance optimization occurs under continuous sensory feedback from the ears, the eyes, the muscles, tendons, joints, and skin. The integration of this information into movement patterns is the most important step in procedural learning. It is mainly based on the formation of neuronal networks, for example, connections between auditory and motor areas and a stepwise reduction of cortical activity and augmentation of subcortical activity in the basal ganglia and the cerebellum. Furthermore, anticipation of the acoustic effects of the intended movements – the efference copy – is crucial. By comparing sensory feedback with anticipated movements and their acoustic effects, it allows sound production to be improved and sensory-motor programs to be continuously optimized in the course of practice (Altenmüller et al., 2022)

Initially, this sensory and auditory information is stored in short-term memory, with the consolidation into long-term memory occurring during breaks or sleep, a critical process for encoding learned motor sequences. Altenmüller suggests that complex tasks should be tackled in shorter practice sessions interspersed with longer breaks, which also emphasizes the importance of sleep as well for memory consolidation. A recent pilot study (McCrary et al., 2022) designed an app to predict and alert musicians to fatigue, prompting them to cease practicing. This is crucial because practice fatigue or over-practicing often results in diminished improvement and can lead to poorer motor movements, potentially reinforcing incorrect procedural memories.

I end this chapter, quoted from Altenmüller's 2018 paper: "As emphasized above, the complex neurophysiological processes involved in musical training and expert performance are not restricted to sensorimotor brain circuits, but also involve memory, imagination, creativity, and—most importantly—emotional communicative skills. The most brilliant virtuosos will not move their listeners if imagination, color, fantasy, and emotion are not part of their artistic expression. These qualities are often not trained solely within a practice studio but depend on and may be linked to experience from daily life, human relationships, a rich artistic environment, and emotional depth. Such factors that profoundly influence the aesthetic quality of music performance can be subject to expertise research; however, they are presently inaccessible to neuroscientific methodology. Important steps here will include the development of more fine-grained imaging technologies and the integration of findings from brain morphology, nerve cell metabolism, connectivity measures, and neurotransmitter activities, at the individual level. Along with experimental paradigms that include meaningful behavioral measures, such research may eventually enable us to uncover the secrets of musical creativity and its emotional power."

Memory

As discussed, through synaptic plasticity neural circuits are refined and strengthened, allowing for the encoding and retention of new information. For music performance, music memorization is an important and unavoidable task. We will take a look at brain plasticity's role in memory – encoding, storage, consolidation, and retrieval. Recall that long-term memory can be broken down into explicit (declarative) and implicit (procedural) systems. Implicit networks comprise of areas such as the premotor, cerebellar, and basal ganglia. Explicit networks are broken down into semantic (the memory of facts, the "what"), and episodic (the "where and "when") memories. The episodic memory system holds events – traces of memories that have associated places, times, emotions and other knowledge based off of an experience. It's a mechanism which is a reconstruction of the past based on retrieved and new information. Episodic networks are complex and take from temporal, parietal, and frontal brain regions – a widely distributed network. So, we can say that episodic memory has an important role in remembering spatial and temporal contexts of an event.

Performing music demands that expert performers effortlessly tap into their long-term memory for musical information while simultaneously managing the ongoing performance in their working memory. It also entails skillful initiation and control of intricate movements, simultaneously monitoring the outcomes and feedback from these actions for necessary adjustments. We explore the challenges posed by music performance on memory retrieval and motor control. In Brown (2015), this paper states that "at least two different types of memory are crucially involved: long-term memory refers to the ability to store information and working memory refers to the ability to retrieve, maintain, and manipulate previously learned information."

To recall music effectively during performance, expert musicians leverage their knowledge of harmonic, metrical, and hierarchical music structures. Performance accuracy is influenced by adherence to musical conventions, with pitch errors fitting the structural context. Similar to memory skills of other experts, musicians excel at recalling well-structured music compared to random sequences. They prioritize essential musical elements like downbeats and primary melody notes. Moreover, musicians excel at perceiving and reproducing expressive variations typical for a given musical structure. The use of "cognitive schemas" or generalized knowledge aids musicians in memorizing and retrieving pieces during performance. Additionally, musicians rely on individual interpretations shaped during rehearsals, expressing consistency while differing from other performers. These interpretations, influenced by expressive intentions, contribute to unique performances. Expert musicians develop mental maps during rehearsal, using key points and expressive features as cues for automatic retrieval, ultimately enhancing accuracy and individuality in their performances. Expert musicians also plan music in sections or in chunks or groups, rather than one task event at a time, which enables their working memory to keep up with their performance in real-time.

The musicians' ability to imagine music is closely tied to auditory-motor integration during musical performance. They demonstrate proficiency in vividly imagining both musical sounds and movements, even in the absence of auditory input or physical performance. This skill is likely honed through their extensive experience with listening to and performing music, as well as forming associations between sounds and movements. When musicians imagine these sounds, subtle motor responses like subvocalizations and activation of motor circuits in the brain are observed. Additionally, experts' proficiency in musical imagery may be connected to their long-term and working memory. Tasks involving auditory and motor imagery often require musicians to actively retrieve music from long-term memory and hold that information in working memory. Differences in mental imagery have been associated with variations in working memory capacity and the ability to suppress interference from other tasks while performing music. For expert musicians, the skill of musical imagery is closely linked to their ability to remember and associate the sounds with the corresponding actions for that music.

Before delving into the intricacies of memory processes in music, it is essential to understand the fundamental principles of the human memory system, which comprises several distinct systems. Initially, there is sensory memory, which briefly retains sensory stimuli without any processing, interpretation, or encoding. Following this is short-term memory, where information is held for a limited duration without undergoing manipulation. Next and crucial to music processing is working memory. Working memory is central for all cognition, in which its functions are termed “maintenance and manipulation” (Oxford, 2018). Working memory is pivotal because it manipulates information that has been held and it is strongly related to executive functions, such as pattern recognition, long-term memory encoding, problem solving, and creativity (Oxford 2018). Due to its diverse functions, working memory is not dependent on a singular focal point, but rather operates as a distributed system encompassing multiple brain regions.

Studies illustrate that music processing involves a series of stages starting from the separation of sounds in the auditory stream to the identification and combination of different acoustic features, and ultimately to memory-related cognitive activities that elicit personal and emotional responses. Listening to music is seen as a hierarchical process in which the auditory stream (serial information organized in tones and chords) is converted into parallel form, which means these tones in series are grouped into melodic segments, and these segments into complete melodies. Throughout this process, working memory plays a critical role by temporarily storing and continuously manipulating musical information. Furthermore, these processes allow the listener to store and recall various auditory elements like pitch, intervals, timbre, and rhythm, which are then integrated to form a cohesive memory of the melody.

Regarding pitch memorization, a study was conducted revealing that non-musicians performed surprisingly well in distinguishing whether the second-to-last or last pitch of a tone sequence matched the first, achieving 66 percent accuracy ding pitch memorization (Gaab et al., 2003). Analysis of fMRI data during pitch memory tasks unveiled that proficient task performance correlated with activation not only in the auditory cortex but also in the parietal lobe (specifically, the supramarginal gyrus) and the cerebellum. Analysis of fMRI data during pitch memory tasks unveiled that proficient task performance correlated with activation not only in the auditory cortex but also in the parietal lobe (specifically, the supramarginal gyrus) and the cerebellum.

When we listen to music, we process and merge sequences of sounds as they arrive. This process requires us to temporarily store auditory information and link it with subsequent sounds to form a melody. Our understanding of musical structure helps us knit these tones into cohesive melodies. Without this ability, following and comprehending even brief pieces of music would be unachievable. This is where maintenance and manipulation of working memory comes into play – the working memory stores information in multimodal code, in which the executive and attention control networks navigate the interactions between working and long-term memory.

According to Thaut and Hodges (2018), the "classical working memory model" is based on the storage of verbal information and lacks clarity on whether phonological loop processing extends to non-verbal information, such as music (pitches, chords, timbres, etc.). The text discusses how verbal information in working memory involves internal articulatory rehearsal (phonological loop), raising the question of whether a similar rehearsal process exists for musical elements like pitch and timbre. Oxford notes that "not many studies have been conducted to date trying to answer this question." While some studies yield mixed results, there is evidence suggesting that tonal working memory may also involve internal rehearsal, particularly when the musical elements are sufficiently familiar and distinct for effective maintenance by the listener. Neuroimaging studies have shown an overlap in neural underpinnings for working memory with both verbal and tonal information – this includes areas such as the fronto-parietal network such as Broca's area, parietal areas, and the planum temporale.

Episodic musical memory is the ability to identify a piece of music while also recalling the specific details of the environment in which it was first heard—such as the time, place, circumstances, and people present (spatiotemporal context). A specific type of episodic musical memory is autobiographical musical memory, which is triggered when we hear music that is closely linked to personal experiences from our past. "The different facets of musical memory have been the focus of substantial research in recent years. Based on this research, we now know that the different musical memory systems mentioned earlier can be modulated by different psychological aspects comprising (1) intrinsic musical features such as timbre or tempo, (2) the emotional and arousal components, and (3) individual schemas and musical structure. A further issue influencing music memory processes, which incidentally is relatively new, pertains to the (4) particular brain activation pattern during encoding and retrieval of music information" (Thaut & Hodges, 2018). This last point is of particular interest to me and will be further explored in the subsequent sections of this chapter on memory.

Music that elicits emotional arousal tends to be more effectively recalled than pieces with minimal emotional impact. This phenomenon can be attributed to two primary factors: the involvement of the mesolimbic system and the heightened associations within the semantic associative network. The mesolimbic reward system is a key pathway in the brain that is primarily involved in the processing and regulation of pleasure and reward. It originates in the ventral tegmental area (VTA) of the midbrain which contains dopaminergic neurons, and projects to various regions, notably the nucleus accumbens which contains dopamine receptors. The nucleus accumbens, NAcc, is found in the ventral striatum, which in turn is part of the basal ganglia. This system releases dopamine, a neurotransmitter that plays a central role in mediating motivation, pleasure-seeking behaviors, learning, reward, and addictions. Other mesolimbic structures the VTA projects to are the amygdala and the hippocampus. This speaks to the significance of dopaminergic processes - "Dopamine is thought to strengthen the synaptic potentiation in memory networks activated during learning and consolidation of the music material. Thus, dopamine also promotes plastic adaptations in brain areas involved in the control of trained and practiced tasks" (Oxford, 2018). Furthermore, another neurotransmitter, serotonin, is also involved in processing music. When music is pleasing to the listener, it's been found that serotonin levels are much higher.

In his 2018 study, Jäncke reveals that "only a few studies have examined the neural underpinnings of music memory so far". Some fMRI studies have reported analogous findings, with bilateral activation in temporal regions in areas such as the primary and secondary auditory cortices in the superior temporal gyrus, along with frontal brain areas. Although these studies use fMRI, Jancke states the measurements are suboptimal for more nuanced evaluation of cognitive processes, and only very short musical excerpts were used. The author writes, "In future experiments it would be extremely helpful to study the neural underpinnings of the different music memory systems using silent and less annoying neurophysiological measurement techniques, such as EEG, MEG, or NIRS which provide the possibility of working with natural music stimuli. Currently, there are no studies using the types of experimental paradigms that were used in the aforementioned fMRI studies. Thus, it is of utmost importance to study the neurophysiological oscillations, intracortical current densities, and coherences during music memory tasks. This would provide the opportunity to study the neural underpinnings of music memory processes using more natural experimental situations…these studies partly correspond with fMRI studies in showing that music perception (and thus partly music memory) is controlled via a distributed neural network binding together brain systems involved in auditory, memory, attention, sequence processing, and executive functions."

A study and meta-analysis in 2017 by Talamini, Altoe, Caretti and Grassi was conducted to see whether or not musicians would out-perform non-musicians in various memory tasks. They used 29 studies which had 53 different memory tasks, and using Hedges' g, measured the effect size. They found that indeed musicians outperformed non-musicians in memory tasks, with a small effect g=0.29 for long term memory, g=0.57 (medium effect) for short term memory, and g= 0.56 for working memory. They suggest two possibilities for this outcome, one being the Pygmalion effect, and two – simply put, musical training "positively influenced (1) auditory processing, (2) improved overlapping neural networks for speech and music functions, and (3) active learning strategies, such as chunking and sensorimotor integration" (Jancke, 2018). Musicians could use their improved auditory processing abilities for more efficient auditory encoding, thus helping with memory. Another factor contributing to musicians' proficiency in memory tasks is the overlapping neural networks involved in music processing, as discussed previously. As music performance involves multiple modalities, such as sound, notation, and motor skills, it fosters the development of robust and more efficient neural association pathways.

Music has also been utilized to bolster memory consolidation in healthy participants. In a study by Judd & Rickard (2010), as reported by Jäncke, the effects of listening to music excerpts on the memory consolidation of verbal material were examined. Following the presentation of verbal material, participants underwent either a 20-minute or 45-minute waiting period during which they relaxed and listened to music. A week later, their retention of the material was assessed. Regardless of the emotional valence of the learned material, it was discovered that memory was significantly enhanced when music was played 20 minutes after learning, but not immediately after or 45 minutes later. This phenomenon was attributed to the 'time course of memory consolidation' - "Memory consolidation is time-dependent since the biochemical processes modulating synaptic processes need some time (at least 25 minutes) to develop and to install the new and altered synaptic contacts in the memory networks, including the release of various hormones into the bloodstream (i.e., epinephrine, norepinephrine, and cortisol)". This aspect of time course of memory consolidation is taken into account when proposing a preliminary design for an experiment explained later in this chapter.

In music, cognitive adaptations play a pivotal role, particularly evident in problem-solving and memory. Musicians exhibit a remarkable ability to recall musical material, surpassing non-musicians, especially when the material adheres to tonal rules (Ericsson, Snyder 2016). This advantage is the result of the culmination of expertise-driven adaptations in memory, including the refinement of working memory capabilities – Ericsson (2018) states, "This skill-by-structure interaction, demonstrated also in other domains, documents that experts' advantages are largely due to their knowledge and how their memory skills have adapted to the structure of the stimuli. Most likely, some of the gains can be attributed to a development of working memory". Gruhn & Rauscher (2002) further advocate for exploring diverse learning processes, highlighting their profound impact on cognitive representations and, consequently, musical performance outcomes. The authors further suggest "the study of individuals' cognitive representation of musical structure is important for understanding how music performance works, because it helps to understand why certain mistakes happen and in which way a good use of the knowledge can be supported…But also from an educational point of view it is relevant to know how different learning processes or methods may result in different representations (Gruhn & Rauscher, 2002)."

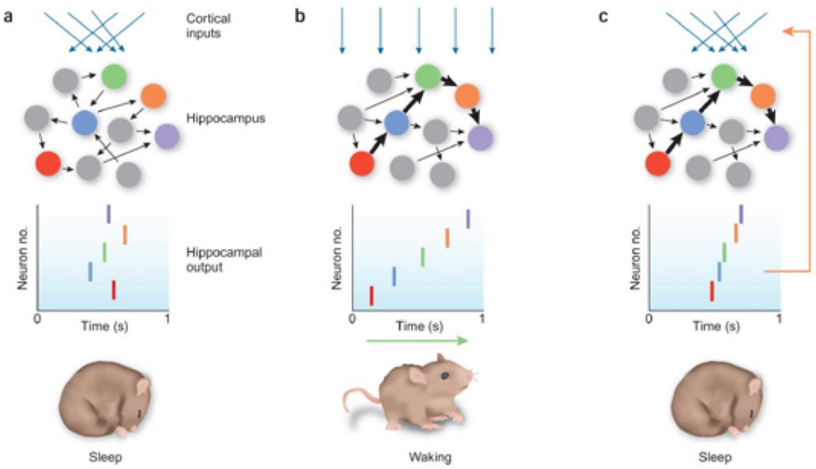
Experiments have shown hippocampal neurons that have been "listened" to. They have shown that hippocampal neurons indeed code for what, where, and when of events or tasks that were given to animals. Hippocampal neurons show how navigation, memory, and planning are all tied together. When we navigate through space, hippocampal neurons create an internal "map" of our location when specific neurons fire at specific locations. With navigation, there is selective location firing of specific cells. For example, if I navigate around a city, there are certain neurons that will prefer to fire at specific locations, and over time will continuously fire at those locations. In the following figure, the square represents place fields, the area that is moved around, and the colored dot represents the place cell, the specific neuron that fired in that place. All together, each square is a representation of a single cell, firing at a specific location. Therefore, the hippocampus contains neural representations of space.

In Mizuromi's experiment, it was discovered that past memories influence the neural representations of space in the hippocampus – if the cells will fire or not in the place field. Place fields are affected by reward and choice outcome, as the hippocampal neurons understand and can distinguish between events (Smith & Mizumori, 2006). As well, Gil et al 2010 demonstrated temporal ordered firing when rats were waiting in between trials. During the intertrial interval, cells were still firing when the rats were in the same environment but not completing the task, suggesting that episodic networks are still active for periods of time afterwards even if the task or event has completed. John O'Keefe and Lynn Nadel (The Hippocampus as a Cognitive Map) state that there are indeed place fields, but these are also based off sensory and motivational cues which are the components of specific events, and which is what distinguishes between different episodes/memories).

We've established that place cells will fire in specific locations, which are impacted by sensory and motivational cues – now the question is whether place cells are temporally organized, that is, do they fire in the same order at specific times? Studies have shown that the hippocampus indeed codes information as a function of time. Mehta (2007) ran an experiment wondering if the hippocampus organizes context information across time – they found that it is. They tracked firing neurons when a lab rat was sleeping, when the rat was walking, and when the rat subsequently slept after walking. They discovered something fascinating – when the rat was sleeping, the same place cells fired in the same order at the same time – this displays that these place cell firings were ordered temporally, dependent on the experience.

Figure 14

Hippocampal cell firings during wake and sleep



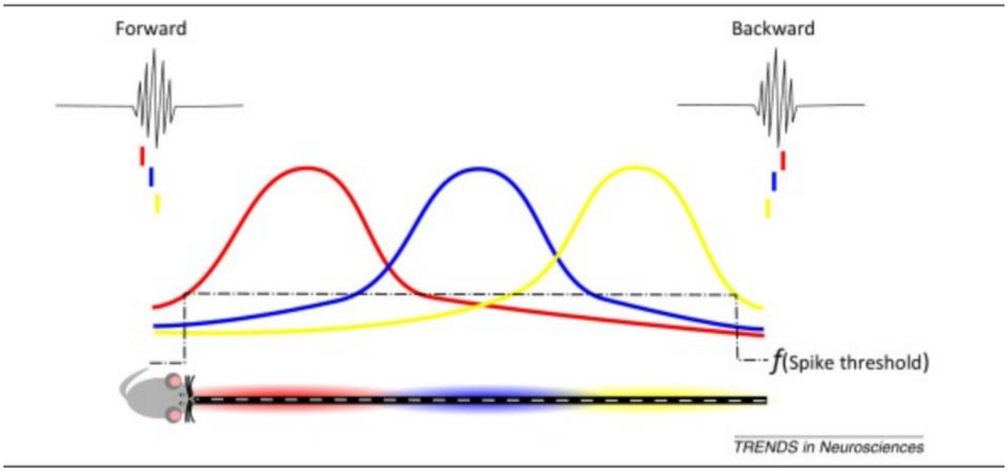
Note. From Cortico-hippocampal interaction during up-down states and memory consolidation by M.R. Mehta, (2007).

Therefore, place fields were expressed in a sequential order. Diba and Buzsáki (2007) created another experiment, suggesting that past experiences reflect the place cell firing order sequencing. They looked at rats before and after tasks, noticing that activation patterns were created even before the task was going in, as the rat was waiting but had experience from previous trials. This showed that the rat was "pre-playing" a sequence of behaviors, even before the tasks began again. These place cells would fire ahead of time from past experienced behavior, but then what they also noticed was that these cells would fire again after the task but in backwards order – the termed this as "replay" – fascinating. This leads to the question of how place fields could be linked in this way – perhaps temporally? Kneirim (2000), created with a concept to explain this phenomenon using synaptic plasticity principles – essentially, when a rat would walk along a path, each place cell would fire along the path. The more times this is completed, synapses between each firing strengthen, so when one cell fires, the next follows suit.

In essence, it has a triggering effect on subsequent place cells. Atherton (2015) describes this as once the synaptic strength is high enough and place cells are now firing in temporal order, each place cell is already at a higher threshold which triggers the following place cell. The lingering excitability of the last firing neuron triggers a backwards replay.

Figure 15

Pre-play and re-play



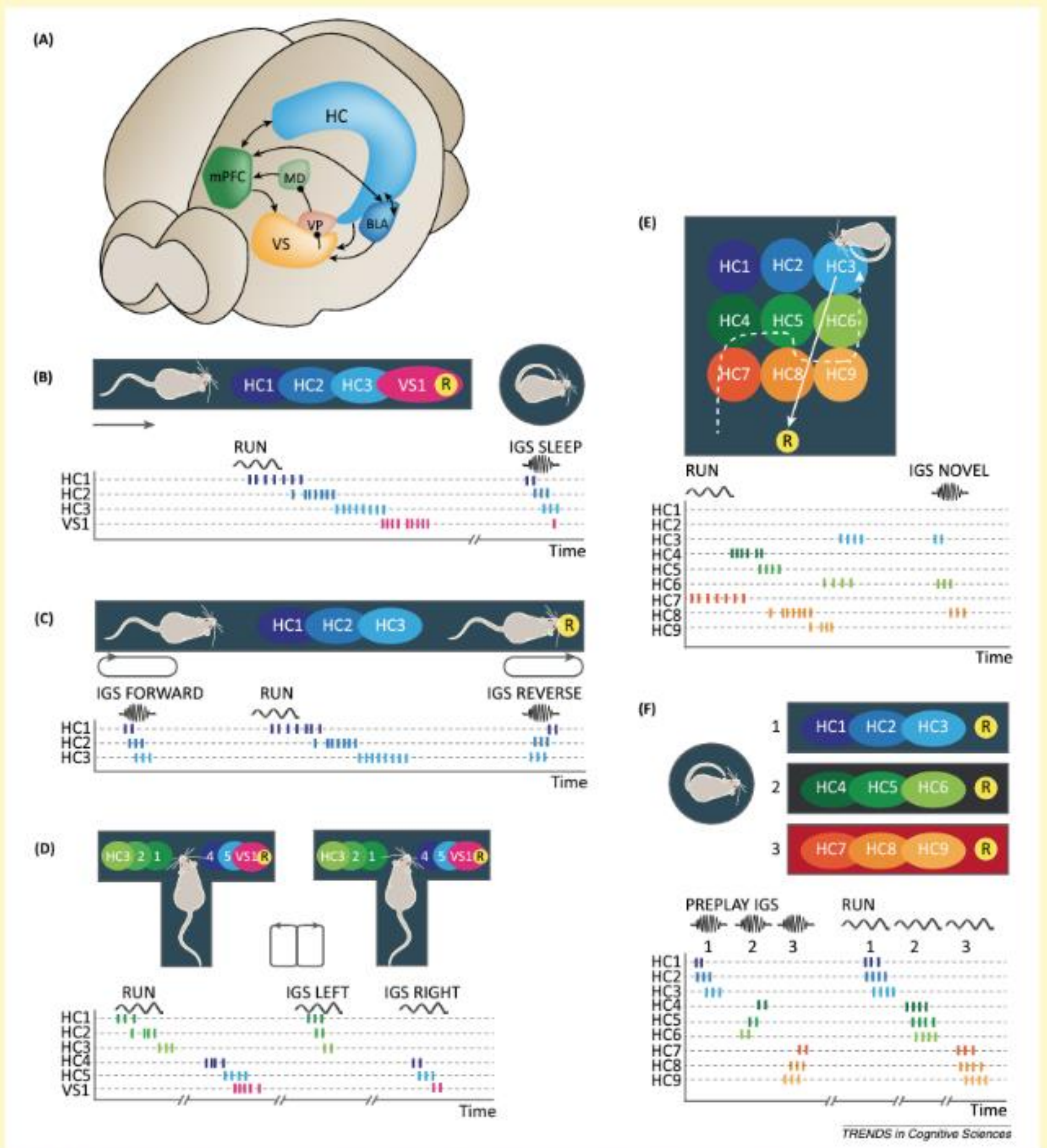
Note. From "Memory trace replay: the shaping of memory consolidation by neuromodulation" by Atherton et al., 2015.

The idea of pre-play and the expectation of the same events occurring is an interesting area of study. In pre-play, under the same circumstances the rat had the same expectation, therefore the same place cells fired before it receives its reward – food, which also coincides with a release of the neurotransmitter dopamine. However, when there was no reward, a mismatch signal fired. Without dopamine reinforcement, this memory could weaken over time. So, the sequencing of these place fields could be reinforced by desirable vs non-desirable outcomes or strengthened or weakened sequences.

Atherton et al. (2015) also propose that “we have identified dopaminergic release during, for example, novel environments and reward driven spatial tasks, as being important for biasing the content of subsequently replaying trajectories, potentially to strengthen new place cell assemblies and place-reward associations”. In another example, Pezzulo et al. (2014) demonstrates dopamine’s effects as a neuromodulator in memory. In this experiment, rats made their way toward the reward, while hippocampal and ventral striatum neurons fired (ventral striatum neurons receive dopaminergic projections from regions such as the VTA/basal ganglia). We see the pre-play during task firings, and replay, all of which are internally generated sequences. However, it is interesting to note that pre-play components helped the rat generate novel routes when driven to a reward – the rat knew the elements involved, so it created a better route to seek the reward. The authors were also able to view the internally generated model when the rat was sleeping.

Figure 16 (next page)

Dopamine drives novel route making



TRENDS in Cognitive Sciences

Figure I. Brain areas involved in goal-directed behavior and classes of IGSs. **(A)** Schematic of brain structures contributing to goal-directed behaviors as represented in the rodent brain. Projections between areas have been depicted with arrows (excitatory) and broken lines (inhibitory). (B–F) IGSs can be classified by their resemblance to the neuronal activation patterns during a behavioral experience. **(B)** As a rat runs along a track (RUN), hippocampal neurons (HC 1–3) are activated at specific locations (blue ellipses), whereas a ventral striatal neuron (VS1) is activated (magenta ellipse) around the reward location (R; yellow dot). Spike patterns during track running and sleep are plotted below the track schematic. During periods of rest and sleep after the running experience neuronal firing patterns are replayed in a forward direction (IGS SLEEP). The replayed IGSs are associated with SWR events in the HC local field potential, while theta oscillations (6–10 Hz) are the dominant rhythm during running. IGSs are compressed in time and may contain spikes from several brain areas including VS. **(C)** Awake replay. When a rat initiates a new journey on the track neuronal patterns can be replayed in a forward direction (IGS FORWARD). By contrast, when a rat pauses at the completion of a journey, IGSs can be replayed in a reversed direction (IGS REVERSE). **(D)** IGSs representing different available future options are generated at decision points on a track (IGS LEFT & RIGHT). These 'forward sweeps' are associated with theta oscillations. The same neurons were activated before when the rat explored both routes on the track (RUN). **(E)** Novel goal-oriented IGSs can be constructed from patterns of place cell activity generated during previous trajectories when a rat initiates a new route towards a goal site (yellow dot, R). Note that the order of the novel IGS does not correspond to the activation order of place cells during the journey of the rat into the arena (RUN; colored circles along dashed white line) but to the place cells that will be activated along the route leading to the goal (colored circles along solid white line). **(F)** Different possible place cell sequences [preplay IGS 1 (HC 1–3), 2 (HC 4–6) and 3 (HC 7–9) are preplayed during sleep or awake periods before a rat enters a novel track (either IGS 1, 2, or 3)]. Sequences preplay in forward or reversed order in equal probabilities. The sequences generated before entry on the novel track were not activated during preceding exploratory behavior of the animal. Abbreviations: BLA, basolateral amygdala; HC, hippocampus; IGS, internally generated sequence; MD, mediodorsal thalamus; mPFC, medial prefrontal cortex; SWR, sharp wave-ripple; VP, ventral pallidum; VS, ventral striatum.

Note. From "Internally generated sequences in learning and executing goal-directed behavior" by Pezzulo et al., 2014.

So, thus far we've seen how the hippocampus represents memories in spatial and temporal processing as networks of cell activity. The question now is, how this information is then transferred to be used in other regions of the brain?

To do this, we take a broader look at the brain. When we look at EEG scans, it can be decomposed into several different frequency bands – theta (4-10 Hz), alpha (8-13 Hz), Beta (13-30 Hz), and Gamma (30-120 Hz). When we look again at Diba and Buzsáki's figure, there are short bursts of condensed gamma oscillations – these are called short wave ripples (SWR) – studies have looked at SWR and their correlation to memory and learning. Norman et al 2019's research suggested SWR and its relationship to recall. They showed pictures to people and after pauses were asked to recall – it was found that SWR's were prominently found when subjects were asked to recall pictures. More interestingly, the peaks of SWR were found right before the recall, and the numbers of SWRs coincided with the accuracy of the subjects' answers, suggesting SWR's correlation to predicting the accuracy of recall. This demonstrates the importance of SWR in learning and memory – furthermore, other experiments demonstrated that when SWR was disturbed during sleep, this led to poor or impaired performance of recall tasks (Girardeau et al 2019). As well, prolonging SWR led to improvements of memory accuracy (Fernandez-Ruiz 2019). Dopamine release also affected SWR positively (Ishikawa et al 2014).

Theta oscillations have been found to be equally important in memory and learning. Research shows that as place cells are firing, theta oscillations are almost 'in sync' with each peak of cell firing, synchronized with theta rhythms. This suggests that theta oscillations could be helping in the organization of cell firing or spatial information. In relation to theta waves, the hippocampus and prefrontal cortex (PFC) have been found to both exhibit theta oscillations. In demanding tasks, it was found that the HPC and PFC were exhibiting synchronized oscillations of the theta band, in which cells were firing in coherence with each other. These coordinated theta findings are interesting because they correlate to when animals do higher order tasks like decision making and problem solving. Igarashi (2015) found that theta oscillations could help coordinate distal brain processing – as a task was being learned, there was low coherence, and improving as tasks got easier, and finally when tasks were mastered coherence was achieved.

Discussions surrounding memory and learning, specifically about pre-play, replay, and expectations brings to light aspects that relate to mental training. In one study by Bernardi et al. in 2013, their aim was to see if mental practice would affect the memory performance of a piece of music. Their definition of mental practice as a technique is "a mental representation of a preconceived idea or action in order to enhance performance." Their subjects were 16 right-handed pianists, split equally between females and males, that were recruited from the University of Music and Theatre in Hanover, Germany. Their goal was to perform a memorized, simple piece of music using either MP methods (whatever method they prefer) or physical practice (PP) methods. On the first day, each subject took 30 minutes to complete MP of the piece, and during this time every 10 minutes were given a short questionnaire about the mental practice strategies they used, rating the types of strategies they used on a Likert scale from 0 through 5. The subjects were questioned if they used the following strategies: mentally hearing the sound of notes, mentally feeling the movement of fingers, visualizing finger movements, visualizing the score, harmonic analysis, rhythmic analysis, and melodic analysis. This was followed by the memory performance. After that, they were given 10 minutes for both MP and PP, along with another questionnaire and a final memory performance. The PP group were given the same 30 minutes to practice, followed by a memory performance, another 10 minutes to practice again along with a second questionnaire, and a final performance.

Figure 17

Mental Practice vs. Physical Practice Design

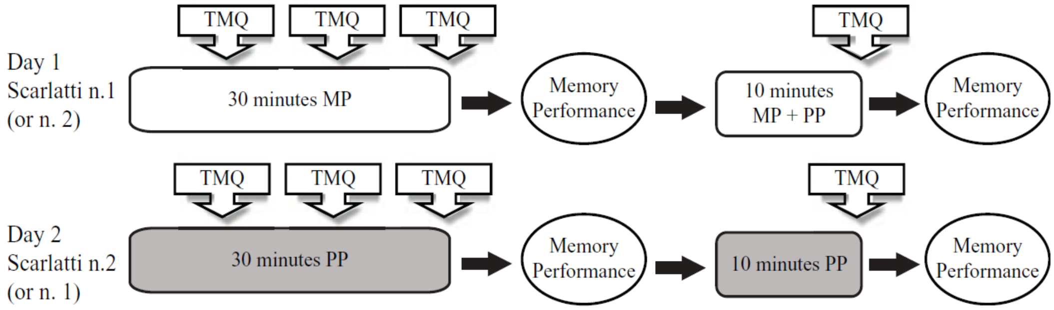


FIGURE 1. Experimental design.
Note. MP = Mental Practice. PP = Physical Practice. TMQ = Ten Minute Questionnaire, administered during practice, aimed at describing the mental strategies being used.

Note. From “Mental Practice in Music Memorization: An Ecological-Empirical Study” by Bernardi et al., 2013.

The researchers hypothesized that a structural analysis of the piece and pitch imagery would be highly beneficial for a positive result, whereas motor and visual imagery would play a minor role, and listening to auditory models would have a negative effect on the result. Researchers discovered that in the MP group, mental practice achieved between 40-60 percent of PP, but the combination of MP and PP practice led to the best results. This is extremely interesting from a musician’s perspective, because mental training has been a part of my personal training but has never been taught as a fundamental need in music schools. This, paired with the concept of pre-play in memory and learning, could lead to a practice strategy which promotes practice away from the piano.

Figure 18

Mental Strategies during Bernardi et al. experiment

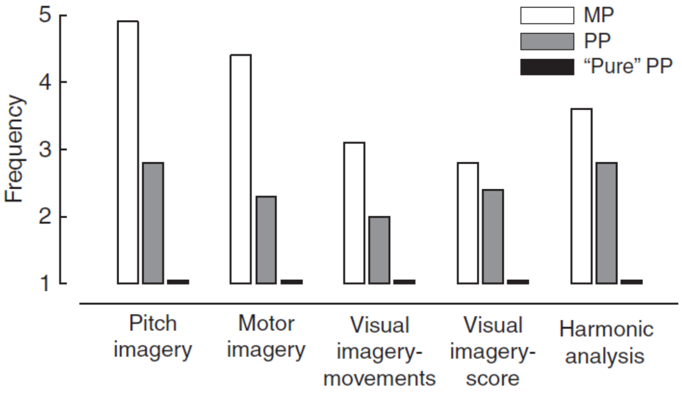


FIGURE 3. Mental strategies used during practice.
Note. Averaged reliance on different mental strategies in different practice condition, derived from averaged TMQ data. All mental strategies are used maximally during mental practice (MP). However, also physical practice (PP) is accompanied by imagery strategies, significantly more than one would expect in a hypothetical practicing condition with no use of imagery ("pure" PP).

Note. From "Mental Practice in Music Memorization: An Ecological-Empirical Study" by Bernardi et al., 2013.

Relating back to memory and neuromodulators such as the neurotransmitter dopamine, Ferreri et al. (2021) investigated the impact of musical rewards, which induce dopamine release, on memory function following consolidation periods. Prior research indicated that a greater enjoyment of music correlates with improved memory recall. Ferreri and colleagues aimed to delve deeper into the underlying mechanisms of these observed behaviors. They conducted a double-blind experiment on 29 participants of both sexes. This investigation tested the manipulation of synaptic dopamine availability, giving dopamine precursors (levodopa), dopamine antagonist (risperidone), or a placebo to participants. After creating these three conditions, participants had to remember musical excerpts after a consolidation period. Their main finding indicated that dopaminergic synaptic availability does indeed impact reward-driven episodic memory, with sensitivity to musical reward playing a crucial role. This relates directly back to discussing theta oscillations, and how this coupling could also be affected by neuromodulators such as dopamine. Dopaminergic regions such as the ventral striatum had strong responses to pleasurable musical input. This supports research on how rewards can enhance dopaminergic pathways and therefore memory. This also supports how dopamine is necessary in long-term memory processes.

Figure 19

Effects of dopamine vs controls on retrieval processes

Figure 1. Schematic representation of the pharmacological intervention and the music memory paradigm.

Note. From “Dopamine modulations of reward-driven music memory consolidation” by Ferreri et al., 2021.

Williamon et al.’s study in 2004 touches upon the concept of attention salient stimuli stimulating the information processing circuit (recall acetylcholine, the nucleus basalis, and auditory cortex).   In this experiment, researchers hypothesized that pianists would utilize structural analysis of a piece of music as part of the encoding and retrieval process. In this study, 6 experienced pianists participated in a visual recognition memory task. They were required to learn J.S. Bach’s Prelude in a minor, BWV 889, from WTC II. None of the participants had played this piece before, and there were no limitations on practice sessions or hours of practice. After each performance, the subjects were questioned on their memorization and practice process. EEG data was collected, and ERPs were identified based on structural and nonstructural metrics. Previous research indicated that pianists, irrespective of their proficiency level, tended to focus their practice on structural aspects, a tendency most pronounced among highly skilled musicians. Williamon further states that neural responses to structural cues differ from those elicited by correct stimuli unrelated to musical structure. These findings align with the long-term memory theories, suggesting that musicians “develop and leverage domain-specific retrieval structures based on generally accepted characteristics of associative encoding and retrieval”. This investigation confirmed that important musical structures were crucial for the encoding and retrieval memory process.

Figure 20

Structural, non-structural, and non-prelude bars used for attentional cues

Fig. 1. Examples of structural, non-structural, and non-prelude bars presented to participants as part of the stimulus set. The entire set consisted of the 32 prelude bars and a matched set of 32 non-prelude bars.

Note. From “The Role of Retrieval Structures in Memorizing Music” by Williamon & Valentine, 2002.

There have also been studies investigating the effects of sleep on music memory consolidation. This may also relate to previously discussed material on the pre-play aspects involved during sleep in mice, perhaps helping with memory consolidation. Simmons conducted a study to explore how rest intervals between practice sessions influence sequence learning among musicians. Drawing from memory consolidation theories dating back to Oerhn in 1895, which emphasized the beneficial effects of rest on performance, she delved into the existing research, particularly focusing on sleep-based consolidation. Notably, there was a gap in published studies regarding the performance of experienced learners in relation to rest intervals. Simmons aimed to fill this gap by investigating whether rest intervals between practice sessions could enhance both accuracy and speed of performance. Her findings revealed that while sleep-based memory consolidation contributed to improved performance accuracy, the observed speed enhancements could also be attributed to consolidation processes occurring during both wakefulness and sleep.   Participants were recruited from the University of Texas at Austin and were 291 music majors with minimal experience or training on the piano beyond 5 semesters of undergraduate group piano classes. There were three conditions to this experiment: one group received 5 minutes rest between sessions, another group 6 hours of rest (including wake-time based consolidation), and the final group 24 hours (rest intervals included both sleep and wake-based consolidation). All three groups demonstrated better performance in the second session, and both wake and sleep-based consolidation participants showed enhanced speed as well. The author indicated some problematic variables though, such as small sample sizes and competency too early in the experiment.

This literature aligns with many teaching scenarios I have encountered while instructing piano lessons to both young children and adults. In my experience teaching K-12 students in local studios or privately, as well as adult students at the University of Washington and Seattle University, I have observed recurring concepts related to memorization. The literature addresses the ideas of explicit and implicit learning. It appears that young children adopt an implicit approach to learning, which correlates with a critical learning period, while adults tend to use a more explicit approach. Consequently, I have found that attentional cues such as structural, harmonic, and visual prompts are particularly beneficial for adult learners struggling with memorization. Additionally, I have observed that mental training – studying the musical score without physically playing the instrument – is highly beneficial for memory consolidation when physical practice at the instrument has already begun, or even before. This suggests that practice away from the piano can be just as important as practice at the piano to establish vivid memories of theoretical, musical, and emotional components of a piece.

Research completed so far on memory has led me to propose a preliminary experimental design which builds upon previous studies. As stated in the Oxford Handbook, there has not been much studied that helps relate neuroscientific or music cognition to help educators. Also, in studying hippocampal place fields relating to memory, to my knowledge I have not seen any studies completed on hippocampal firing on human subjects playing the piano. It would be interesting to see how studying the temporal and spatial sequencing of hippocampal place cells during a piano performance task could help with understanding music memorization and practice strategies. In particular, it would be intriguing to see if understanding hippocampal sequencing could give way to understanding repetitions required in a performance task, or the ideal interval of rest between repetitions in a single practice session over the course of a month (for example). This type of study could also give way to understanding improvements for implementing mental training, how brain plasticity aids in mental training or how mental training could provide a scaffolding effect for future learning.

I have proposed a general framework and possible questions for this preliminary study. Research questions may include - what happens when you add other factors like attentional cues (do the place fields fire any differently)? How does adding emotion, like fear, induce hippocampal firing remapping (in rat experiments, inducing fear remapped hippocampal cells firing even if the direct environment did not change). How does rest affect memory learning and consolidation - does replay happen as well after playing music? This is due to the concepts of anticipation and expectation which are also involved in memory (ex. cells firing during pre-play before a task, anticipating the subsequent firing of the next cell in sequence). Also, research has demonstrated dopamine as a strong neuromodulator – does inducing release of dopamine in between task sessions increase the firing of cells?

Research participants or subjects:

From studying the literature so far, I would propose narrowing down subjects between age, musicians, non-musicians, length of training, start of training, and socioeconomic status. Participants would then be divided into separate control and test groups.

Methodology:

Literature has shown that longitudinal studies show causation vs. cross sectional studies that deal mainly with correlation. I would opt to use electrophysiological methods such as EEG to interpret neuron cell firings, but then also pair this with fMRI imaging to analyze any changes in regions that are active during the performance and memorization process. Ericsson (2018) elaborates on methodological approaches, stating that “the ideal way to determine factors influencing skill development is to collect longitudinal data over a period of time that is thought to capture behaviors relevant to skill attainment. This method allows analyses of practice histories of successful and less (or non-) successful individuals without biases associated with assessing an already successful sample. This type of research affords high predictive validity because it allows some statements about causality (rather than just relationships). Because of the nature of longitudinal research, that is, it is time consuming, subject to high dropout, and difficult to perform when the aim is to include young individuals who are expected to make it to adult-elite levels, this technique is not commonly used. For this type of research to be most successful, large sample sizes are required, especially if the follow-up period is significantly removed from the initial period of data collection."

Method:

Participants are assigned short musical piano excerpts. The control group is just asked to simply play the musical excerpt. Group 2 is given attentional visual cues, such as structural markings in the score and colors before playing the excerpt. Group 3 is asked to practice the excerpt backwards. Group 4 is asked to go for a walk in nature for 10 minutes (dopamine induction) between practice iterations. Finally, participants will be asked to recall the excerpt, and we will see overall which group recalls with more accuracy.

Results:

The interest is in the pattern of cell firing within the hippocampal neurons relating to the overall effect. With attentional cues, will this induce greater firing of cells and greater accuracy? For Group 3, does practicing the excerpt backwards (imitating re-play) induce better performance overall? In Group 4, does the increase in dopamine into the system also induce accuracy? Future considerations: Previous studies have shown that memory and creativity are linked – it would be interesting to see if understanding the spatial and temporal firing of hippocampal neurons could affect our understanding of the underlying mechanisms behind creative work and performance.

Motor Skill Acquisition

Motor learning is a complex process that involves the acquisition and refinement of skills through practice and experience, fundamentally grounded in neurobiological mechanisms. At its core, motor learning engages multiple brain regions, including the motor cortex, cerebellum, and basal ganglia, which work together to encode, store, and retrieve motor patterns. This neural interplay facilitates the development of muscle memory and the fine-tuning of motor skills. In this chapter, we will explore the intricacies of motor acquisition with a particular focus on bimanual coordination. Additionally, we will delve into the role of mental practice and imagery, examining how these cognitive strategies can enhance motor performance and learning without physical movement. By understanding these fundamental aspects, we can gain deeper insights into the neural underpinnings of musical skill development and the ways in which musicians optimize their practice for peak performance.

Upper and lower motor neurons are distinct in terms of their origins, synapse points, pathways, neurotransmitters, and the effects of any lesions. These motor neurons are part of complex and regulated circuits responsible for voluntary and involuntary movements through muscles and glands. The system involves two types of neurons: upper motor neurons (glutamatergic), which start in the cerebral cortex and project to the brainstem or spinal cord, and lower motor neurons (utilizing acetylcholine), which originate in the spinal cord and extend to muscles and glands across the body (Zayia, 2003). To execute voluntary movement, the initiation of a signal occurs within the primary motor cortex. The motor cortex is located in the frontal lobe, divided into the primary and non-primary areas. The primary motor cortex is found in the precentral gyrus, located anterior to the central sulcus, while the non-primary areas are divided into pre-motor and supplementary motor cortex. This region contains the upper motor neurons, Betz cells, integrate both excitatory and inhibitory inputs from the cortex. They translate this integrated information into a coherent signal that either instigates or suppresses voluntary movement.

Motor skill acquisition begins with a series of neural processes that involve multiple brain regions, with the motor cortex playing a pivotal role. Initially, sensory input is processed in sensory areas of the brain and then relayed to the prefrontal cortex, where movement planning occurs. The supplementary motor area (SMA) and premotor cortex are also crucial during this cognitive stage, as they prepare and organize the necessary motor sequences. As learning progresses into the associative stage, the primary motor cortex (M1) becomes critically involved. Located in the frontal lobe, M1 is responsible for executing voluntary movements by sending signals through the corticospinal tract to the spinal cord, activating relevant muscles. With repeated practice, the synaptic connections in M1 are strengthened, making motor activity more focused and efficient. The cerebellum plays a significant role in refining these movements, ensuring they are smooth and coordinated. It receives input from the motor cortex and sensory systems and provides feedback to correct and fine-tune movements, facilitating real-time adjustments. In the autonomous stage, the basal ganglia become essential for developing motor habits. These nuclei help transition movements from conscious and effortful to automatic and effortless. As skills become more practiced, the basal ganglia streamline these movements, reducing the cognitive load required. As discussed in previous chapters, long-term potentiation (LTP) and neural plasticity in the motor cortex and other areas lead to more efficient neural circuits. This synaptic strengthening results in permanent changes that enable the automatic performance of motor skills with minimal conscious thought. Throughout the learning process, the motor cortex integrates information from various regions, including the sensory cortex, premotor areas, cerebellum, and basal ganglia, resulting in a well-coordinated and efficient neural network for executing complex motor tasks smoothly.

Motor skill learning, as discussed by Luft and Buitrago (2005), progresses through several distinct stages, each characterized by unique neural mechanisms and patterns of brain activity. Initially, in the acquisition phase, skills are vulnerable to interference, requiring repeated sessions for consolidation. Behavioral evidence shows that simple skills can be learned quickly, while complex skills need spaced training over days, with sleep playing a crucial role in self-rehearsal and performance gains without further practice. The involvement of different brain circuits varies across stages: early learning activates association areas for visuospatial-motor associations, in which complex movements may require both motor and spatial encoding systems to operate simultaneously utilizing the “mirror neuron system” (Luft & Buitrago, 2005). Later stages engage cerebello-striato-motor cortex loops for movement efficiency. Within-session learning exhibits habituation effects, while intersession learning results in increased and more efficient primary motor cortex (M1) activation. Interference from learning new tasks can disrupt the consolidation of previously learned skills, though this resistance to interference strengthens over time. Overall, different brain regions, including the prefrontal cortex, striatum, and cerebellum, contribute variably across these stages, highlighting the dynamic nature of motor skill acquisition and consolidation.

The motor cortex plays a critical role in planning, controlling, and executing voluntary movements. In the realm of performance, pianists must skillfully integrate sensory feedback with motor commands to produce aligned movements across both hands. This level of control demonstrates the complexities of bimanual motor skill acquisition, illustrating how dedicated practice refines neural pathways to support enhanced motor output and artistic expression.

Therefore, researching the specific challenges and neural adaptations involved in piano-related bimanual coordination not only deepens our understanding of motor learning but may also benefit educational strategies and rehabilitation techniques.

Haslinger et al.'s 2004 bimanual coordination study explores how professional pianists manage complex bimanual motor tasks compared to individuals without musical training, employing functional magnetic resonance imaging (fMRI) to monitor brain activity. Participants, comprising 12 professional pianists and 12 musically untrained "naïve" controls, performed designed bimanual tasks that simulated performing piano scales, involving both mirrored(in-phase) and parallel(anti-phase) finger movements. Analysis generated from fMRI data revealed that professional pianists showed significantly lower brain activation in key motor control areas such as the dorsal premotor cortex, supplementary motor area, and cerebellum. This suggests a higher neural efficiency in pianists, which is likely the result of extensive training and practice. Behavioral measures, such as reaction times and movement synchrony, did not show significant differences between the groups, demonstrating that the motor efficiency was specific to neural activity rather than general motor performance. The implications of these findings are twofold. They contribute to our understanding of how continuous and intense practice can lead to neuroplastic adaptations that enhance the brain's efficiency for specific skilled activities. Furthermore, enhanced motor proficiency potentially allows professional pianists to allocate cognitive resources to more advanced aspects of musical performance, such as emotional expression and musical interpretation.

Swinnen and Gooijers' paper (2015) delves into cognitive processes underlying the coordination of both hands, focusing on how constraints – neuromuscular, temporal, spatial, and cognitive – affect performance. They highlight that neuromuscular constraints dictate the ease of certain movements, such as the stable in-phase coordination where both hands move symmetrically, in contrast to the more challenging anti-phase movements which require opposing actions and often lead to a shift back to in-phase under increased speed or complexity. Temporal and spatial constraints challenge the synchronization of movements as well, demanding higher cognitive input and sophisticated neural interplay, particularly involving the corpus callosum, which facilitates interhemispheric communication. The authors discuss the brain's adaptability through practice, which can reshape neural pathways to overcome these constraints, thereby enhancing the efficiency and complexity of bimanual actions, as evidenced by reduced cognitive load and optimized motor control in skilled individuals such as musicians.

Hwang et al.’s 2021 research echoes the findings of Haslinger et al., demonstrating the brain's remarkable ability to adapt and enhance efficiency in response to change. The authors investigate how the motor cortex's involvement evolves with long-term training in motor performance, using mice trained to perform joystick movements in two directions. In this experiment mice were trained over several weeks to move a joystick in forward and downward directions, with their performance and motor cortex dependency assessed through various stages of learning. The study found that as mice became proficient in these movements, the involvement of the motor cortex diminished, particularly for movements that the mice performed with greater consistency and precision. The paper further outlines the role of the primary motor cortex (M1) in learning and executing skilled movements, highlighting that not all movements rely on an intact M1. The discussion elaborates on how movements initially dependent on the motor cortex can become more distal with sustained practice, emphasizing a shift in neural activity patterns within M1 during extended training. The "consistent-direction" movement, in which mice performed with higher precision and reliability, exhibited reduced M1 activity compared to the less consistent "variable-direction" movement. These findings suggest that the motor cortex's role in executing well-learned movements decreases as performance becomes more consistent and movements become more automatic, reflecting a significant reorganization of motor circuits away from M1 dependency to potentially other brain regions.

A study by Furuya et al. (2013) complements findings from previous research by further demonstrating the brain's capacity for neuroplastic adaptations in response to motor skill training. The authors investigate the impact of piano practice at submaximal speeds on the maximum speed of finger movements. The experiment involved musically naïve participants who were divided into a training group and a control group. The training group practiced a sequence of piano keystrokes at a submaximal tempo over four days, while the control group did not engage in any practice. The results demonstrated that the training group significantly increased their maximum speed of finger movements, not only for the practiced sequences but also for similar unpracticed sequences, indicating intra-manual transfer of skill. However, this increase in speed did not transfer to the untrained hand, suggesting that the improvements were specific to a region. The study highlights the importance of slow practice in enhancing the maximum speed of skilled movements, showcasing the potential of such practice regimes in motor learning and suggesting a basis for therapeutic approaches in conditions like focal hand dystonia. This research underscores the brain's capacity to optimize motor function through targeted practice, enhancing our understanding of motor learning dynamics. The research focused on how practicing piano at submaximal speeds can affect the maximum speed of finger movements. The study involved twelve musically naive young male adults who were divided into two groups: a training group and a control group. Over four consecutive days, the training group practiced a specific sequence of piano keystrokes using their non-dominant left hand. This sequence consisted of twelve strokes that utilized all possible finger pairs, and each participant repeated this sequence fifty times per day. The sequence was played at a predefined tempo, coordinated with a metronome set at two strokes per second, ensuring that the practice tempo was slower than the participants' maximum speed. The control group did not engage in any practice. To assess the effects of the training, both pre-test and post-test sessions were conducted for all participants, measuring the Inter-Keystroke Interval (IKI) - the time between keystrokes - as a proxy for the speed and accuracy of their finger movements. These tests included playing the practiced sequence as fast as possible, performing similar unpracticed sequences, and other tests to measure intra-manual (within the same hand) and inter-manual (between hands) transfer effects. The results showed that after four days, the training group significantly increased their maximum speed of the practiced finger movements and demonstrated improvement in performing similar, but unpracticed sequences, suggesting intra-manual skill transfer. However, this increased speed and proficiency did not transfer to the untrained hand, highlighting the effector-specific nature of motor learning.

Garbarini et al. (2014) also explored bimanual coupling. Their research involved subjects drawing lines with one hand while either drawing or imagining drawing circles with the other hand. The study utilized a combination of behavioral analysis and fMRI to assess how motor performance and brain activity differed between congruent (drawing lines with both hands) and non-congruent (drawing a line with one hand and a circle with the other) tasks. Key findings revealed that non-congruent tasks, both real and imagined, induce significant changes in motor performance, characterized by spatial interference where the movement trajectories tend to merge. This effect was mirrored in the brain's activity; particularly, a prefrontal-parietal network involving areas like the pre-Supplementary Motor Area (pre-SMA) and the posterior parietal cortex (PPC) was more active during non-congruent tasks. These regions are crucial for the planning and execution of complex bimanual movements, supporting the idea that both actual and imagined movements engage similar neural circuits dedicated to managing dual motor tasks. The importance of this research lies in its demonstration of how the brain facilitates complex bimanual tasks, not only during physical execution but also in a purely cognitive or imagined space. This insight expands our understanding of motor control and could inform therapeutic strategies for motor rehabilitation, highlighting the brain's capacity to adapt motor outputs based on imagined scenarios, which can be critical for patient recovery when physical movement is limited.

An interesting study by Sobierajewicz et al. (2017) aimed to investigate whether the repeated imagination of a fine motor sequencing skill leads to sequence-specific learning and if motor imagery shows EEG patterns similar to those observed with actual sequence execution. In this study, 24 right-handed participants between the ages of 21-28 practiced or imagined specific response sequences using a modified discrete sequence production (DSP) Go/NoGo task while EEG was recorded. The task involved pressing or imagining pressing keys in response to visual stimuli. The experiment was divided into two phases: the practice phase, where participants completed four blocks of 96 sequences (40 executions, 40 motor imagery, 16 control), and the test phase, which included 72 sequences (60 executions, 12 withheld). During the practice phase, participants practiced specific sequences under the conditions of motor execution, motor imagery, and a control where they withheld responses. In the test phase, participants executed all sequences, both familiar (practiced) and unfamiliar, to assess learning effects. The sequences were indicated by visual stimuli, followed by a preparation interval and a Go/NoGo signal to either execute, imagine, or withhold the sequence. The literature review highlights the distinction between sequence-specific learning (learning a particular sequence) and sequence-a-specific learning (general sequencing skill), which are crucial for understanding motor learning processes. During the experiments, subjects were shown a fixation cross followed by a series of five yellow squares indicating the sequence of key presses. Each square was displayed for 750ms, with a subsequent preparation interval of 1500ms. Participants were then given a colored cross (green for Go, blue for motor imagery, red for NoGo) to signal whether they should execute, imagine, or withhold the sequence. Throughout the tasks, EEG was recorded from 128 channels to capture brain activity, and EMG was measured to ensure no muscle activity during motor imagery and control conditions.

During the practice phase, subjects showed significant improvement in response times (RT) and accuracy (percentage correct, PC) across practice blocks. The first key press was consistently slower, indicating segmentation of the sequence into chunks. During the test phase, subjects performed better on familiar executed and familiar imagined sequences compared to unfamiliar sequences, indicating sequence-specific learning. The results indicated that motor imagery can induce sequence-specific learning, as participants performed better on familiar sequences compared to unfamiliar ones.

In EEG data, event-related potentials (ERPs) displayed similar activation patterns for motor execution and motor imagery above central motor areas, supporting the idea that motor imagery activates similar neural processes as actual movement. Event-related lateralizations (ERLs) illustrated more negative activity on contralateral motor areas during both motor execution and imagery compared to the control condition, indicating motor-related brain activation.

Figure 21

Topographical map of ERPs for motor execution, motor imagery vs controls.

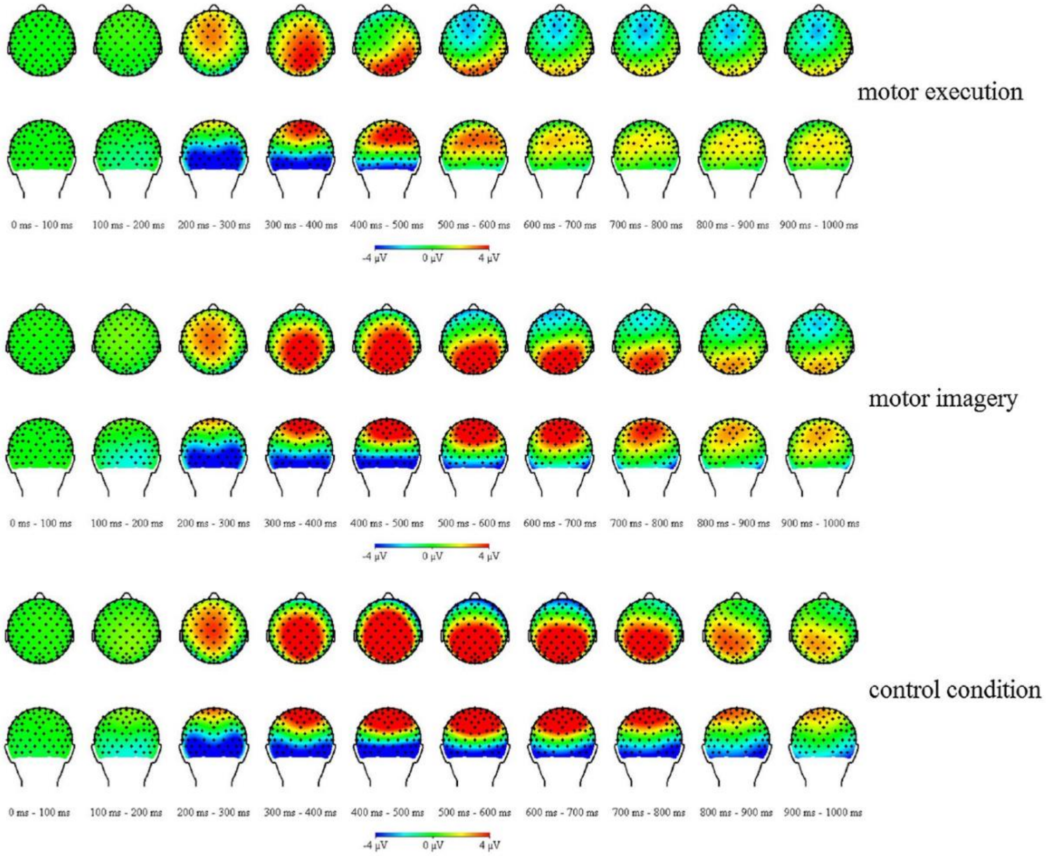


Fig. 7 Topographical maps of event-related potentials (ERPs) for motor execution, motor imagery, and control condition trials in the practice phase from the Go/NoGo signal (0 ms) to 1000 ms after the Go/NoGo signal

Note. From “The influence of motor imagery on the learning of a fine hand motor skill” by Sobierajewicz et al., 2017.

The authors present topographical maps of ERPs for motor execution, motor imagery, and control conditions during the practice phase from the Go/NoGo signal (0ms) to 1000ms after the signal. It displays ERPs exhibited maximum amplitudes above central sites, with distinct patterns of brain activity for each condition. Specifically, the motor execution and motor imagery tasks showed reduced positivity, indicating activation of motor areas, whereas the control condition, where participants had to withhold responses, showed stronger positivity, which is interpreted as motor inhibition. The results highlight the similarities in brain activation patterns between motor execution and motor imagery, suggesting that imagining movements engages neural processes similar to those used during actual movement execution.

EEG and EMG analyses showed that motor imagery and motor execution shared similar activation patterns in motor-related brain regions, supporting the notion that motor imagery activates similar neural processes as actual movement and that the results were due to mental simulation rather than physical movement. This finding is significant for motor learning and rehabilitation, suggesting that motor imagery could be a valuable tool for improving motor skills, especially in situations where physical practice is limited. Future research should focus on identifying factors that enhance the effectiveness of motor imagery training. This relates directly to piano performance or music performance in general, as mental training exercises should be incorporated during the motor learning phase of musical pieces.

Along similar lines, the idea of motor imagery can extend to the idea of external focus during a musical performance, as researched in a paper by Williams et al. (2023). This 2023 study explores the effects of an external focus of attention on musicians' skill acquisition using the Audiation Practice Tool (APT). The literature review references Gabriele Wulf's research over the last 20 years on attentional focus for motor learning, which has extensively demonstrated that an external focus of attention - directing attention towards the intended movement effect rather than the movements themselves - enhances learning and performance across various motor tasks. The authors state that "focusing on technical aspect and thinking about how to play a phrase during playing involves declarative processes that are too slow and cumbersome, as well as a high cognitive load". Movement science and Wulf's findings have been well-documented in sports and physical activities, but their application in music pedagogy, particularly in naturalistic settings, remains underexplored – "As both sports and music involve complex movements there are compelling reasons to extend the research into the benefits of external focus to the field of music" (Williams et al., 2023). Within the field of music, according to the authors external focus is "anticipating the desired effect of one's movements…imagining the movements of the instrument's mechanisms, the sounds that are about to be created, or the expression of the sounds", and that the "more expert the performer, the more distal the focus should be". Williams et al. also express that imaging sound should be "clear, vivid, rich, and multi-modal" to achieve maximum effectiveness.

Figure 22

Internally focused aspects of performance vs. externally focused concepts

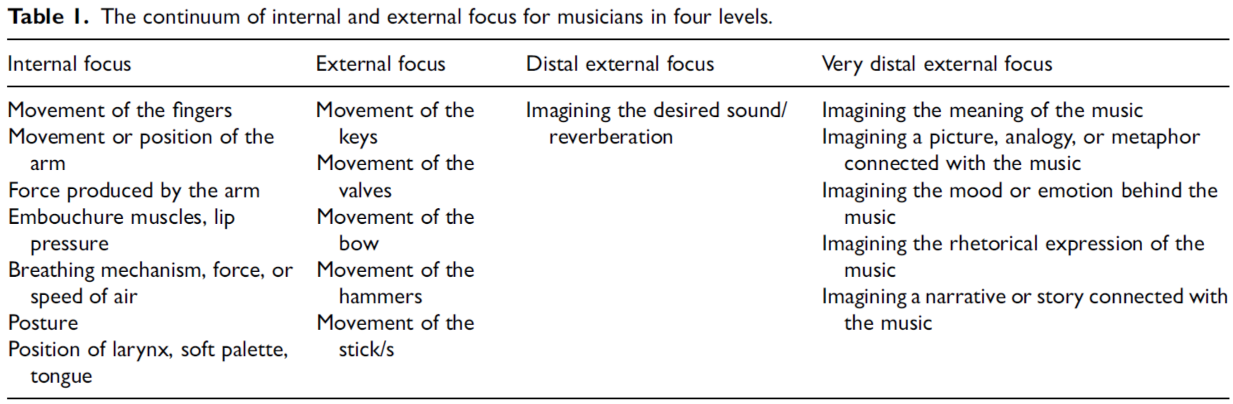


Table 1. The continuum of internal and external focus for musicians in four levels.

Internal focus	External focus	Distal external focus	Very distal external focus
Movement of the fingers Movement or position of the arm Force produced by the arm Embouchure muscles, lip pressure Breathing mechanism, force, or speed of air Posture Position of larynx, soft palette, tongue	Movement of the keys Movement of the valves Movement of the bow Movement of the hammers Movement of the stick/s	Imagining the desired sound/ reverberation	Imagining the meaning of the music Imagining a picture, analogy, or metaphor connected with the music Imagining the mood or emotion behind the music Imagining the rhetorical expression of the music Imagining a narrative or story connected with the music

Note. From "Practicing Musical Intention: The Effects of External Focus of Attention on Musicians' Skill Acquisition" by Williams et al. (2023)

The APT consisted of four steps: (a) imagining the musical phrase with nuanced details, (b) singing and gesturing the phrase (c) playing the phrase, and (d) playing another version of the phrase with a different emotion or character. This tool was designed to engage musicians in external focus by involving auditory and kinesthetic imagery. The experiment involved seven conservatoire natural trumpet students who practiced unfamiliar pieces using both their usual methods and the APT. The practice sessions were divided into control and intervention phases. Participants assessed the difficulty of the pieces and their playing condition, practiced the pieces, and completed various questionnaires on performance accuracy, self-efficacy, confidence, motivation, and engagement.

Figures 23

Results

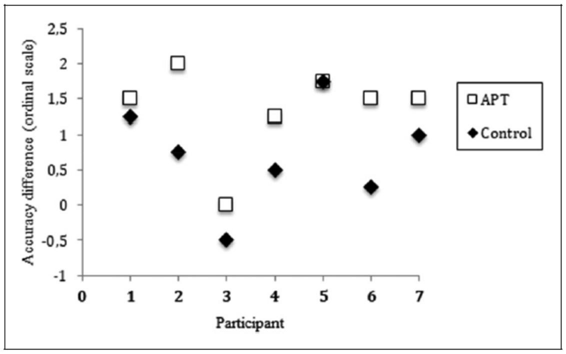


Figure 2. Changes in pre- and post-practice accuracy for the APT and Control phases.
Note. The squares represent the change in accuracy (adjusted scale) for the APT phase for each of the seven participants (horizontal axis), and the diamonds represent the difference in accuracy for the Control phase. Positive values indicate improvement.

Table 6. Individual case studies.

	Participant						
Variable	1	2	3	4	5	6	7
Playing level	High	High	Low	Low	Medium	Medium	Medium
Sight reading (errors)[a]	5	11	42	33	22	21	13
Practice profile[b]	ITE	TI	TIE	TI	TIE	TIE	TIE
Accuracy: control[c]	1.25	0.75	−0.5	0.5	1.75	0.25	1
Accuracy: APT[c]	1.5	2	0	1.25	1.75	1.5	1.5
Self-efficacy: control	74	66	52	30	79	44	64
Self-efficacy: APT	80	56	71	43	77	50	79
Use of the APT after 3 months							
Whole tool	Occ.[d]	Occ.	Daily	Daily	Daily	Never	Daily
Imagining	Daily	Daily				Occ.	
Singing	Daily	Occ.				Daily	
Gesturing	Daily	Daily				Occ.	
Playing variations	Daily	Occ.				Occ.	

Note. Summary of participants as concise case studies.
[a] Sight reading: number of errors.
[b] Practice profile (pre-intervention): I = internal focus; T = technical focus; E = external focus.
[c] Accuracy scores are difference scores, recoded into an ordinal scale.
[d] Occ. = occasionally.

Note. From “Practicing Musical Intention: The Effects of External Focus of Attention on Musicians’ Skill Acquisition” by Williams et al. (2023)

The results showed that practicing with the APT improved performance accuracy compared to their “usual” methods. While improvements in self-efficacy and confidence were not statistically significant, there was a trend suggesting potential benefits. The quantitative scores for motivation and engagement were inconclusive, but qualitative data from exit questionnaires indicated that most participants found the APT engaging and enjoyable. Overall, the study's findings suggest that an external focus of attention can enhance musical performance and learning. However, the study’s limitations and possible changes for future research involve including longer practice phases and larger participant groups to validate these results. Table 6 from the paper illustrates the varied impacts of the APT on individual participants, highlighting trends in improved accuracy and self-efficacy, as well as the sustained use of the tool post-intervention. This suggests the APT's potential benefits for enhancing practice and performance in musicians.

In conclusion, this research on motor skill acquisition indicates the adaptability of the motor cortex in optimizing performance through various techniques. Studies on bimanual coordination demonstrate the brain's capacity to manage complex dual-hand activities, enhancing efficiency and precision with practice. Motor imagery has also proven to be a powerful tool, engaging neural processes similar to those used in actual movement, facilitating skill learning even when physical movement is limited. Additionally, the implementation of an external focus of attention, as seen with the Audiation Practice Tool, highlights the benefits of directing attention towards the intended movement effect, leading to improved accuracy. Collectively, these findings emphasize the potential of integrating these strategies into musical training, performance techniques, and pedagogical approaches.

The aspect of bimanual coordination frequently arises, particularly when novice pianists begin lessons. I have repeatedly observed students struggle when initially learning to play scales in parallel motion. Beginner learners often find it easier to play with both hands in mirrored fashion compared to playing parallel, which aligns with literature discussing in-phase versus anti-phase motions. I noticed that students must exert more mental and physical effort to complete parallel exercises. It appears that an awareness of any changes in melodic sequencing and identifying challenging sections helps students develop better practice habits to overcome the limitations of using both hands at the piano. Another intriguing concept that has aided students in learning and memorizing sequences or sections of music relates to the idea of external focus, as discussed in the literature. I have observed that when students are encouraged to express characters, evoke emotions, or create a narrative for a piece, they tend to perform better and memorize music more accurately and at a faster pace. As a pianist, I have also noticed this in my own practice. When I have struggled with a memorizing music, I have discovered that the key is to focus on the intended sound or intend movement (the bigger picture) rather than on the detailed motor skill itself. This way, I there is a storyline that ultimately keeps spinning and driving the music forward.

Creativity and the DMN Network

The interrelationship between Csikszentmihalyi's theory of flow and the creative process will be discussed, in which contributions to literature on optimal experience will be reviewed alongside ideas relating to musical and non-musical aspects of creativity. Flow, or optimal experience, is defined as "a mental state in which an individual is completely immersed in an activity with a feeling of energized focus and full involvement, without reflective self-consciousness but with a deep sense of control (Csikszentmihalyhi, 1990)" (Araújo & Hein, 2018). For this review, creativity is loosely defined as the ability to make connections between seemingly unrelated ideas in a novel way which produces a product that brings value in a certain field (Bengtsson, Csikszentmihalyi, & Ulléén, 2007). Upon researching flow's relatedness to the creative process, several intertwining themes emerged – concepts of discovery, challenge-skill balance, automaticity, improvisation, divergent thinking, and self-regulation. These themes will demonstrate a unifying relationship between flow and creativity.

Facilitation of flow and creative processes are bound by the idea of constant discovery, novelty, and originality. In Csikszentmihalyi (2014), researchers questioned if "discovery-oriented behavior in real-life situation involving creative production would be related to the assessed creativity of the product." Art students created a still-life drawing during class while their process of creative production was ranked. Results demonstrated a positive correlation between higher discovery behavior and originality/aesthetic value of the product. The strongest correlation was between the discovery of solutions in preparation for the drawing and originality. Routledge, G. Gute, D. Gute, Nakamura and Csikszentmihalyi (2008) discuss the concept of a complex family framework, in which discovery relates to seeking a unique identity and taking on new functions in a family context. They state, "forces of order and novelty result in a coordinated stabilizing and broadening of attention…if channeled and accepted by gatekeepers, might result in ‘breakthroughs’ or creative contributions to the culture or specific domain (Csikszentmihalyi 1999)” (Routledge et al., 2008). In a study examining creative output in the form of music compositions, student groups were given different musical stimuli and discovered different ways to implement these into their work. It was found that there was significant correlation between high flow levels occurring during work and higher quality group musical compositions (MacDonald, Byrne, & Carlton, 2006). In each of these three studies, there was a process of discovery and novelty that led to inducing work “flow”, thereby allowing for creative process and products to emerge.

In flow theory, balance between perceived challenge and skill is an important factor for optimal experience. This is also apparent in the area of creativity. Routledge et al. (2008) analyzed how children’s upbringings with their families could contribute to later creative achievement as adults. Csikszentmihalyi’s family complexity theory has two components: differentiation (movement to uniqueness, change) and integration (support, having common goals and values). Routledge et al. (2008) states having complexity is central to creative persons, and that in “optimized complex systems, these two ongoing processes of differentiation and integration keep the system healthy and growing.” This mirrors flow theory’s challenge-skill factor. In order to keep flow growing there needs to be a balance between difficulty and ability, just like in a creative framework there must be a healthy balance between integration and differentiation: “Rathunde’s findings demonstrated that family context facilitates flow experiences in adolescents by consistently providing experiences that balance choice, clarity, centering, commitment, and challenge…” (Routledge et al., 2008). They also state that integration and differentiation are catalysts for finding optimal experience conditions and for nurturing creative processes. Abuhamdeh and Csikszentmihalyi (2012) demonstrated that perceived challenge produced greater enjoyment in activities that were autotelic – intrinsically motivated activities that were goal-directed. The study involved chess players rating their enjoyment levels after a game finished. Players most enjoyed games in which they outperformed their opponents by a small margin to win the game. Outperforming by a larger margin was not as enjoyable, and games lost against superior players were more enjoyable than wins against inferior opponents. From this research, seemingly oppositional factors of flow work together in creating optimal environments and therefore broadening creative solutions.

Optimal experience also draws upon automaticity and spontaneity in the completion of a task. Dietrich (2018) discusses three distinctions in creative thought – deliberate mode, spontaneous mode, and flow mode. Deliberate mode is associated with conscious processing, signs of agency, intentionality, and planning - conscious reasoning. Spontaneous mode entails opposite attributes - unconscious processing, no agency, effortlessness. However, flow mode requires a physical motion that the other two do not impose. Furthermore, it requires a sense of automatization of motor skills, in which Dietrich (2018) states the following:

> The implicit system is experience based and can only develop a mental representation of the motor task by doing it. In other words, once the motor efficiency that defines flow mode can only proceed from an implicit representation, the motor skill must be well practiced first. This is why novices learning a new skill do not report flow experiences.

There should not be interference in controlling an automated motor skill, or micro-managing of the explicit system, in which its representation is abstract and too slow in real-time. In conclusion, this concept of flow mode is directly related to automaticity in actions, allowing for larger bouts of creative output. Bengtsson et al. (2007) experiments with the concepts of divergent thinking and spontaneity within the area of creating improvisations. Divergent thinking encompasses the ability to generate many possible solutions to an open-ended problem, whereas convergent problems have one answer. Bengtsson et al. (2007) found active brain regions when professional pianists were improvising under fMRI scanners, indicating that musical improvisation could be an important tool in studying creative behaviours. ‘Free’ and spontaneous choice actions that show activity in frontal/temporal lobes demonstrate involvement in creativity and reproduction of tasks. Elaborating on the idea of ‘free’ thought, Gray, Anderson, Chen, Kelly, Christian, Patrick, and Lewis (2018) sought a way to quantity streams of free associations. They found that “forward flow” was highly correlated with ratings of creativity. Gray et al. (2018) state:

> Default network activity also predicts creativity, likely because relatively unconstrained thinking is important for the generation and retention of novel ideas…recent studies support the idea that creativity is related to individual differences in memory organization – differences that allow more creative participants to connect ideas that are further apart in memory.

Flow state also involves good perception of how well one is doing during a performance task. Byrne, MacDonald, and Carlton (2003) examined flow levels and the creative output of musical compositions. Groups of students also employed Csikszentmihalyi’s Experience Sampling Form (ESF) for self-reflection regarding class activities. Researchers found that when flow conditions were met (clear goals, immediate feedback, challenge-skill balance), the quality of the creative product increased at the end. Therefore, there was a significant correlation between optimal experience and creative output. Byrne et al. (2003) states the research provides a “powerful reflective tool for teachers can be developed using the flow model…in initiating, planning, monitoring, regulating, and assessing learning. In other words, flow could be used to manage the learning environment." When students indicated variables and positive factors relating to flow in their self-reflections, their product showed higher results. O'Neill (1999) also relates self-regulation and practice time to higher levels of flow and creativity. Her study also implemented Csikszentmihalyi's ESF method, in which higher achievers experienced flow more frequently, correlating to higher practice times. The implication found here is that educators should find opportunities for their students to reach optimal experience levels.

Overall, the articles mentioned demonstrate a strong relationship between optimal experience and creativity, in both musical and non-musical contexts. It appears that the creative process and products can be the result of being in states of flow. Four main areas demonstrated this relationship. The importance of discovery and novelty led to new creations; a balance of integration and differentiation in a challenge-skill balance framework had great implications on creative achievement; the concepts of automaticity, free thought, and divergent thinking were tied to flow mode and improvisatory ideas; and self-regulation is a tool that can be used to induce greater flow experience and creative output. There are questions that still need to be answered or clarified – Can these deductions stretch into other fields besides the ones discussed in this literature review, and to what extent? As stated, creativity is difficult to define – will neuroscience and psychology's definition of creativity become more absolute in the future? How does one assess creativity in a less biased manner? Is there a definite point in flow mode that one can pinpoint when creative is happening? There are numerous questions to be asked, as flow and creativity are 'divergent' topics in and of themselves.

Underlying these optimal experiences is the interplay of neural networks that facilitate such cognitive abilities. The default mode network (DMN) is a brain network associated with mind-wandering and self-referential thoughts, but increasingly recognized for its role in creative thinking and the integration of complex ideas. Understanding the DMN's function provides valuable insights into how our brains support not only creativity and flow but also the broader cognitive processes that enable these states.

The default mode network was serendipitously discovered when scientists conducting neuroimaging studies began to observe brain regions that were active during the passive control conditions - certain brain regions exhibited consistent activity during rest, rather than when engaged in specific tasks, which contradicted the prevailing assumption that the brain would be largely inactive during rest periods. The discovery of the default mode network (DMN) is attributed to several key figures, including Bharat Biswal, and Barry S. Shulman, and Marcus Raichle, who contributed to understanding the brain's intrinsic activity at rest, though it was Raichle who coined the term "default mode network" in 2001 which described regions active during self-referential and introspective tasks day dreaming and mind-wandering.

In Raichle et al.'s seminal paper "A default mode of brain function", the researchers discovered the DMN by observing brain activity during periods when participants were "at rest" and not engaged in specific tasks. Using positron emission tomography (PET) to measure cerebral blood flow and oxygen consumption, they found that certain brain regions, such as the medial prefrontal cortex and posterior cingulate cortex, remained highly active during these rest periods. Remarkably, this resting activity accounted for about 5% of the brain's total energy consumption, highlighting the DMN's role in maintaining baseline or default brain functions.

Figure 24

Brain regions that change neural activity depending on cognitive demands

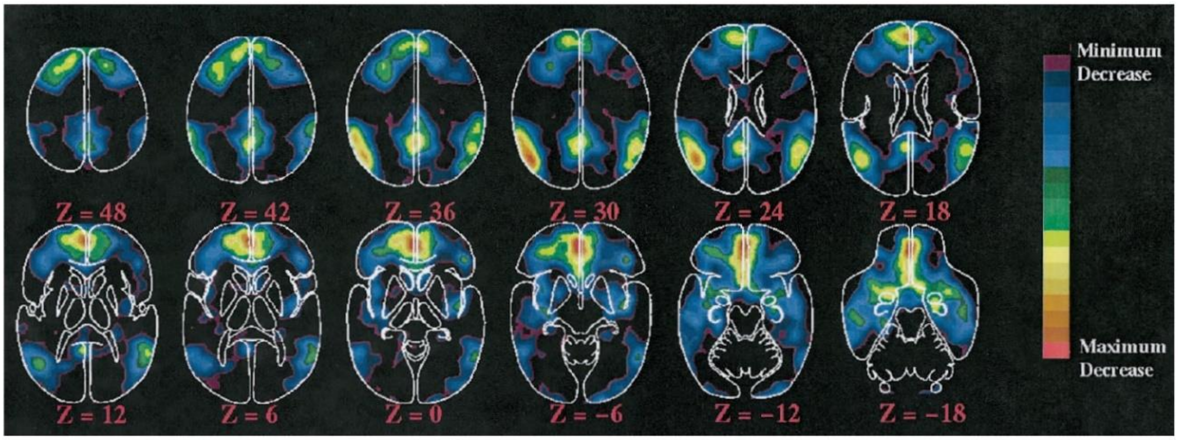


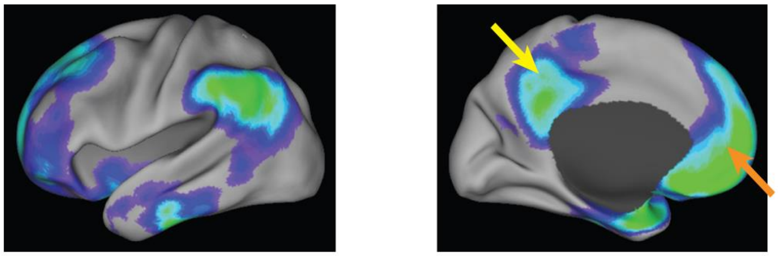
Fig. 1. Regions of the brain regularly observed to decrease their activity during attention demanding cognitive tasks. These data represent a metaanalysis of nine functional brain imaging studies performed with PET and analyzed by Shulman and colleagues (49). In each of the studies included, the subjects processed a particular visual image in the task state and viewed it passively in the control state. One hundred thirty-two individuals contributed to the data in these images. These decreases appear to be largely task independent. The images are oriented with the anterior at the top and the left side to the reader's left. The numbers beneath each image represent the millimeters above or below a transverse plane running through the anterior and posterior commissures (26).

Note. From “A Default Mode of Brain Function” by Raichle et al. 2001

The DMN comprises of activity in certain regions and neural structures, which are active “at rest” and quiet during active states. These are namely the medial prefrontal cortex (mPFC), (which is further broken down into the vmPFC and dmPFC), the posterior cingulate cortex, precuneus nucleus, and the hippocampus as well as the insular cortex.

Figure 25

DMN areas



Note. From Raichle et al., 2015.

Figure 26

Closer look at DMN regions and structures

Note. From “Neural correlates of maintaining one’s political beliefs in the face of counterevidence” by Kaplan et al. 2016.

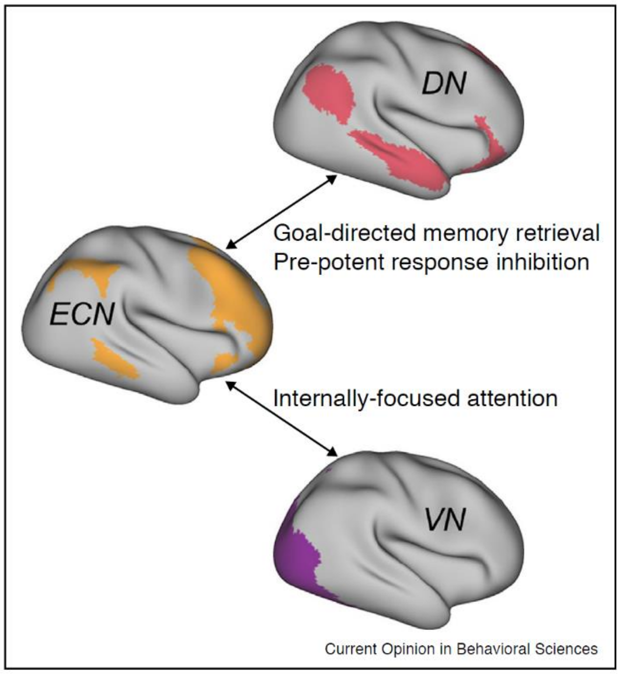
The ventromedial prefrontal cortex (vmPFC) integrates sensory information with response outcomes to determine subjective meaning or significance, while the dorsomedial prefrontal cortex (dmPFC) is involved in self-referential judgments. The precuneus nucleus plays a role in interpreting environmental perceptions, forming strategies, and retrieving episodic memories. Similar to the hippocampus, the posterior cingulate cortex is crucial for the retrieval of autobiographical memories. Additionally, the insular cortex is associated with empathy, metacognition, and the awareness of feelings such as pain. The default mode network (DMN) has been identified in rats, monkeys, and humans (Raichle et al., 2015).

Self-referential thinking, memory retrieval, and the integration of complex information within the DMN prompts curiosity about how it facilitates creative processes and innovative thinking, which are essential for artistic endeavors such as music learning and performance. The concept of creativity and its relationship to the DMN is explored in Beaty et al.’s papers (2016, 2018, 2019). Beaty's research emphasizes that creativity involves generating novel and useful ideas by drawing on and recombining memories. This process is facilitated by the interaction between the default mode network (DMN) and executive control networks. The DMN plays a key role in retrieving and integrating episodic and semantic memories, which serve as the foundation for creative ideation. Meanwhile, the executive control networks help evaluate and refine these ideas, ensuring they are relevant and effective for specific tasks. This dynamic interplay highlights the importance of memory retrieval in creative thinking. Creative cognition research has also been tied to the ideas of divergent and flexible thinking. The authors emphasize the importance of divergent thinking (often measured by Alternate Uses Task), which involves generating multiple unique solutions to open-ended problems and is a key indicator of creative potential. Beaty et al. (2019) describes the elements of divergent thinking as strategically searching episodic memories for relevant information, which is an inwardly focused goal coupled with frontal executive controls that receive guidance (hippocampal retrieval is directed by the frontal executive control network).

Beaty et al. (2018, 2019) investigated the neural foundations of creative thinking by examining brain connectivity patterns. They identified three key brain networks - default mode, salience, and executive systems - that are linked to high creative ability. The default mode network (DMN) supports spontaneous self-referential thoughts, mind-wandering, and goal-directed memory retrieval. The salience network detects significant stimuli, while the executive control network manages response inhibition and attention, essential for reducing interference from irrelevant inputs. This research revealed that highly creative individuals are adept at focusing their attention and suppressing non-salient information to the task at hand, facilitating effective memory retrieval, or “internally focused attention”.

Figure 27:

Networks interact for goal-directed memory retrieval



Current Opinion in Behavioral Sciences

Cognitive mechanisms of brain network interactions during creative cognition. *Notes.* DN = default network; ECN = executive control network; VN = visual network.

Note. From "Network neuroscience of creative cognition: Mapping cognitive mechanisms and individual differences in the creative brain" by Beaty et al., 2019.

In their 2018 experiment, Beaty et al. compared the network profiles of high and low creative subjects during their baseline resting states. They studied brain connectivity in 163 participants, mainly from creative disciplines like art, music, and science. Subjects performed two tasks during fMRI scanning: the Alternate Uses Task (AUT), which involved generating new uses for common objects to assess divergent thinking, and the Object Characteristics Task (OCT), focusing on typical object characteristics as a control. The fMRI data collected displayed high correlation between all three networks, whereas low creative individuals had emphasis on DMN and sensory or cerebellar areas.

Figure 28:

High creative individuals and their connectivity vs. low

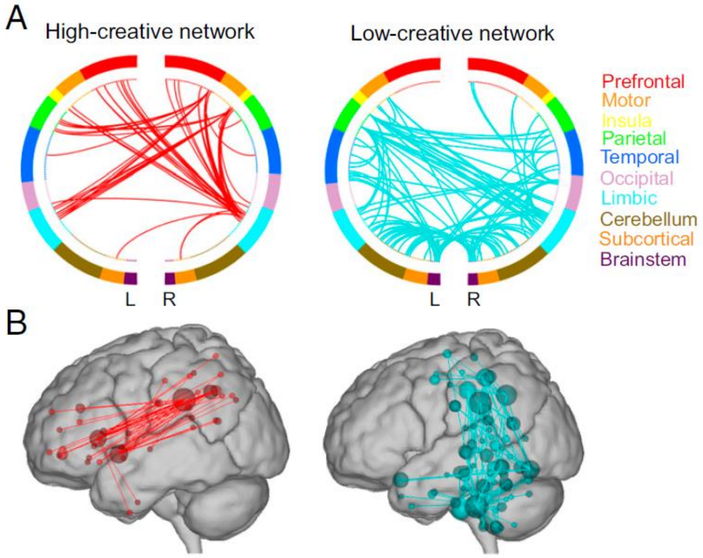


Fig. 1. Depictions of the high- and low-creative networks. Circle plots (*A*) and glass brains (*B*) were thresholded to show the highest degree (*k*) nodes in the networks (high-creative *k* = 10, low-creative *k* = 18). Colors within the circle plots correspond to lobes of the brain. L, left hemisphere; R, right hemisphere.

Note. From “Network neuroscience of creative cognition: Mapping cognitive mechanisms and individual differences in the creative brain” by Beaty et al., 2019.

A literature review and experiment by Rosen et al. (2024) delves into the concept of creative flow, particularly in the context of jazz improvisation. The authors discuss two contrasting hypotheses about the neural basis of flow: one suggesting that flow is a state of optimized task-specific processing resulting from extensive practice, characterized by minimal interference from the DMN, and another proposing that flow involves domain-general associative ideation supported by DMN activity. The review highlights the importance of large-scale brain networks like the DMN and the fronto-parietal control network (FPCN) in creative production, noting that the DMN is typically involved in self-referential thought and mind-wandering, while the FPCN supports executive functions such as working memory and cognitive control – this mirrors and elaborates on the research completed by Beaty et al. (2018, 2019). Their experiment involved 32 jazz guitarists with varying levels of experience, ranging from students to professional musicians. Participants performed six improvisations based on provided chord sequences and rhythmic accompaniment. Each guitarist then performed six improvisations while EEG data were recorded. The improvisations were followed by participants completing the Core Flow State Scale (CFSS) to rate their flow experience. Judges later rated the improvisations on creativity, aesthetic appeal, and technical proficiency. Results illustrated that high-experience musicians in high-flow states showed reduced activity in posterior DMN nodes, while low-experience musicians did not show significant flow-related modulation of DMN or FPCN activity. This supports the hypothesis that creative flow involves optimized task-specific processing facilitated by extensive practice, rather than domain-general associative ideation. The findings suggest that expertise plays a crucial role in achieving creative flow, with reduced cognitive control and specific brain network activity contributing to optimal performance. Both Rosen et al. and Beaty et al.'s studies explore the role of large-scale brain networks in creative processes. While Rosen et al. focuses on how these networks contribute to creative flow during jazz improvisation using EEG, Beaty investigates their role in divergent thinking and creative ideation more broadly using fMRI. While both studies highlight the importance of the DMN and control networks in creativity, Rosen et al. lean towards understanding how minimizing DMN activity can facilitate flow in specialized, high-skill creative tasks such as jazz improvisation. In contrast, Beaty et al. suggests a robust interaction between these networks, supporting a broader range of creative activities. This difference in findings may reflect the different methodologies and creative tasks analyzed, emphasizing the complexity and context-dependency of brain networks in creativity.

The connections between Csikszentmihalyi's concept of optimal flow and the neural workings of the Default Mode Network (DMN) illustrate the complexities of studying creativity. Optimal flow, marked by deep immersion and heightened productivity, is linked to the DMN, which supports mind-wandering, self-referential thought, and imaginative processes. Recent studies have expanded our understanding of how network connectivity within the DMN and its interaction with other brain regions facilitate the generation of novel ideas and creative solutions. Drawing from my personal teaching experience, I have found several of Csikszentmihalyi’s concepts to be highly applicable in the classroom. For instance, when a student selects piano music that exceeds their current skill level, they tend to lose interest quickly and are unlikely to enter an optimal flow state during practice. Conversely, when the student encounters a manageable challenge and can accomplish given technical or musical tasks, they feel encouraged and motivated to continue practicing, finding the experience intrinsically rewarding. This concept is particularly important to consider when selecting new repertoire for performance, and I have specifically kept this in mind when a student presents a piece they wish to work on. Furthermore, I have observed that students with improvisation experience are able to leverage their memorization and flexibility to create more imaginative and creative interpretations of their pieces. This suggests that improvisation should be considered as a vital component of music performance and education.

Conclusion and Strategies

Understanding the neural mechanisms underlying learning and music holds profound implications for music education, performance, and pedagogical approaches. Insight into music perception, including neurobiological mechanisms like Long-Term Potentiation (LTP) and salient attentional stimuli, not only enhances our comprehension of music and language acquisition but also augments memory processes. Furthermore, awareness of neuroplastic changes elucidates how the brain adapts during music acquisition and learning, shaping the effectiveness of musical training and vice versa. Creativity, music, and the Default Mode Network (DMN) share intricate relationships, shedding light on the neural processes involved in creative musical expression.

Delving into these neural mechanisms paves the way for innovative strategies in music learning, memory, performance, and teaching. Insights translated from neuroscientific research inform mental training strategies, emphasizing the significance of attentional cues, the importance of rest intervals between repetitions, and the role of sleep during memory consolidation. Moreover, understanding the interplay between explicit and implicit forms of learning offers nuanced approaches to musical instruction, facilitating more effective skill acquisition and retention. The firing patterns of hippocampal neurons, characterized by their spatial and temporal activity, play a crucial role in memory formation and retrieval. By examining how hippocampal neurons encode and represent spatial and temporal information, researchers can gain a deeper understanding of how musicians remember and recall musical structures, sequences, and performances. This knowledge can inform pedagogical approaches aimed at enhancing memory consolidation and retrieval in musical training and performance contexts.

In music pedagogy, the enduring significance of demonstration and imitation remains important for teaching. While advancements in neuroscience provide valuable insights, the fundamental role of hands-on instruction and demonstration in teaching music is still a significant aspect of successful learning. By synthesizing neuroscientific knowledge with traditional pedagogical methods, educators can craft comprehensive and tailored approaches to music instruction, fostering a deeper understanding, appreciation, and mastery of music among learners.

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