Remembering sounds in the brain: from locationist findings to dynamic connectivity research

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Abstract

Our world is full of sounds, either verbal or non-verbal, pleasant or unpleasant, meaningful or simply irrelevant noise. Understanding, memorizing, and predicting the sounds, even non-verbal ones which our environment is full of, is a complex perceptuo-cognitive function that we constantly refine by everyday experience and learning. Musical sounds are a peculiar case due to their culture-dependent complexity and hierarchical organization requiring cognitive functions such as memory to be understood, and due to the presence of individuals (musicians) who dedicate their lifetime to master the specifics of those sounds and rules. Thus far, most of the neuroimaging research focused on verbal sounds and how they are processed and stored in the human brain. Only recently, researchers have tried to elucidate the neural mechanisms and structures allowing non-verbal, musical sounds to be modeled, predicted and remembered. However, those neuroimaging studies often

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provide only a mere snapshot of a complex dynamic process unfolding over time. To capture the complexity of musical memory and cognition, new methods are needed. A promising analysis method is dynamic functional connectivity, which assumes that functional connectivity changes in a short time. We conclude that moving from a locationist to a dynamic perspective on auditory memory might allow us to finally comprehend the neural mechanisms that regulate encoding and retrieval of sounds.

Keywords: auditory memory, pattern recognition, brain spatiotemporal dynamics, dynamic functional connectivity, music neuroscience.

Introduction

Since we are born, and even earlier, we are immersed in a sound-rich environment and even in a vacuum, we start hearing noises from our own bodies (Kolata, 1984; Parga *et al.*, 2018). These sounds whether verbal or non-verbal, pleasant or unpleasant, meaningful or simply irrelevant noise, constitute the ever-changing stream impinging on our ears and brains and changing them continuously by neuroplastic processes. Thanks to these perceptual-learning and neuroplastic processes commencing even before birth, we possess a complex perceptuo-cognitive function that allows us to understand, memorize, predicting, recognize and finally attribute meaning to sounds (Brattico & Varankaite, 2019; Brattico, 2019; Gebauer, Kringelbach & Vuust, 2015; Hallam, 2018).

Musical sounds are a peculiar case due to their culture-dependent complexity and hierarchical organization requiring several cognitive functions, such as memory and attention, to be understood. Moreover, since thousands of years human cultures and societies nurture and educate individuals (musicians) who dedicate their life to master the specifics of those sounds and rules, resulting in highly specialized auditory processing skills dependent on neuroplastic processes (Altenmüller & Furuya, 2017; Brattico *et al.*, 2021; Reybrouck, Vuust & Brattico, 2018; Criscuolo *et al.*, 2022). To date, however, the psychological and neural mechanisms that permit learning, recognition and memory for complex musical sounds remain unclear.

Most research conducted on learning and memory, though focused on visual and spatial information, has been conducted initially on brain-damaged patients, such as the classical study of Brenda Milner (1966) on H.M. which presented a long-term (LTM) episodic memory deterioration because of the removal of scar tissue on the bilateral hippocampus. Since the ’90s (designated as the “Decade of the Brain” by US President George W. Bush), studies on memory in healthy subjects have become possible thanks to functional techniques, such as magnetic resonance (fMRI), electroencephalography (EEG) or magnetoencephalography (MEG). With these techniques, it was possible to investigate encoding, storage, retrieval, and predictive processes of mainly verbal or visuospatial information, with a small minority of studies on auditory non-verbal or musical information. While providing valuable information supporting and complementing knowledge previously obtained from brain-lesioned patients, the neuroimaging studies focused on regional brain activations, and static connections during memory tasks (Van den Heuvel & Hulshoff Pol, 2010), leaving it open the question on the dynamic fast network changes during memory processes for sounds evolving in time. In this review we wish to first provide an overview of neuroimaging findings on memory for musical sounds and then present the frontiers of research on dynamic connectome for music.

Memorizing sounds over time: the peculiar case of music

Based on the current literature, there is a scarcity of models focused on non-verbal auditory information, since most of the studies focus on visual, verbal or spatial memory. In the following sections we will briefly summarize the main theories that have been proposed to explain the storage mechanisms of non-verbal auditory and musical information, with a focus on different memory systems: sensory memory, working memory (WM) and long-term memory (LTM).

Sensory memory has been measured for the first time by Sperling (1963) and subsequently integrated on the multi-store model of memory by Atkinson & Shiffrin (1968), a theory which postulates that sensory information (auditory information included) passes through sensory and short-term memory storages, before being lost (due to decay or interference) or permanently consolidated on LTM (see also

Broadbent, 1958; Cowan, 1984, 1988), In relation to auditory sensory memory (or echoic memory), for example, it has been demonstrated that subjects are able to recognize differences between two similar sounds only when these sounds are presented less than 10 seconds from each other (Cowan, 1984), with a decline in performance when similar sounds are presented in between as interfering stimuli (Cowan, 1984; Deutsch, 1975; Massaro, 1970). When sounds are separated by a silent period, subjects can compare them only when they are very different from each other. Such degradation of sensory signal appears to comply with the idea that once the memory trace related to the first sound is deleted by the sensory buffer, subjects can rely only on the store having a higher retention range. Store that, however, can contain sound information with much lower resolution than that of the sensory buffer. Most of these results have been obtained with classical paradigms like, for example, the oddball task, which consists in the presentation of repeated stimuli occasionally interrupted by a deviant stimulus.

WM (Baddeley & Hitch, 1974) is defined as the system behind complex cognitive abilities, a system on which cognitive processing and reasoning rely. Auditory WM allows not only to to recognize and to learn the various features of sound (e.g., pitch, tempo or timbre), but also to integrate them in a spectrally and temporally complex way, e.g., for consonance, tonality, rhythm, allowing understanding and appreciation of music (Seashore, 1937). The classical experiments conducted by Diana Deutsch (1999) demonstrated that auditory WM does exactly that: it maintains different sound features, like timbre or pitch, and recombines them for more advanced stages of cognitive processing. One of the most used paradigms used in WM studies, including auditory ones, is n-back of isolated sounds, in which a sequence of stimuli is presented, and the subject is asked to indicate if the current stimulus is the same or different to the stimulus presented N trials back. Another very common paradigm for studying auditory WM is the delayed response task, in which a stimulus is presented and then extinct, and after a variable amount of time the same stimulus and a similar one are presented to a subject, who is asked to identify the original stimulus.

The longest-lasting and largest-capacity memory system is LTM. Numerous experiments have been conducted to understand which sound features (e.g., pitch, rhythm, timbre) are most involved in the recognition of familiar melodies (for example, "Summertime" by G. Gershwin can be recognized simply from the few notes of the incipit). An experimental technique that is often utilized in music memory research is "octave scrambling", which consists in transposing a melody into different octaves while maintaining the order in which the different pitches are presented (Deutsch, 1972). With this technique it was seen that what makes melodies recognizable is the maintenance of the *contour*, that is, the *up* and *down* patterns of the various pitches, even when the melodies are decomposed into different octaves (Dowling, 1978).

Auditory recognition, however, tends to be worse than recognition in the visual (Cohen, Horowitz & Wolfe, 2009) or tactile sensory modalities. Bigelow and Poremba (2014) have examined memory recognition for visual (silent videos), auditory (complex sound of everyday life) and tactile (objects of common use hidden and presented in such a way that they can be touched and manipulated) stimuli, showing that auditory recognition is significantly worse than in other modalities, with no significant differences between visual or tactile stimuli. Cohen *et al.* (2009) have argued that auditory recognition is worse than other modalities due to our tendency to primarily rely on visual stimuli. This might explain why auditory recognition is weaker than visual recognition even among musicians (Cauda *et al.*, 2011).

Despite the classical subdivision between sensory memory, WM and LTM, the formation of new musical memories is an extremely dynamic process, which is the outcome of real time listening and predicting: the notes that we recognize in a melody are continuously unfolding and varying during listening and can be understood only based on the models and priors we have accumulated from life exposure to sounds (Dowling, Tillman & Ayers, 2002). Crowder *et al.* (1989) have conducted a study in which participants compared the pitches of a sine tone followed by a tone played by a musical instrument, evidencing that discrimination was faster the more familiar participants were with the timbre of the instrument. This might be due to the fact that LTM generates a mental image of the frequency of the pure tone as if it had been played in the timbre of the instrument used for the second sound. This and other findings inspired Cowan (1988, 1998, 1999) to propose that long-term memory consists of specialized subsystems or activation mechanisms that process (auditory) sensory features of the stimulus alongside its long-term categorical representation. Although Cowan's models assume that some sensory features are maintained for longer periods of time, they do not explain the apparent contradiction between the classical findings on the limitations in accessing sensory information and its long-term retention. Even for recall, the melodies are never perfectly remembered note by note, but small variations are often produced, which remain metrically and harmonically coherent with the original (Sloboda, 1985). Hence, episodic LTM for melodies consists in the memorization of abstract patterns in which not necessarily all the superficial details are kept (Snyder, 2009). What remains of these details, however, has been a long controversial topic. Some theories are based on the idea of the importance of hierarchical structures, in which some musical events are structurally more important than others (Deutsch & Feroe, 1981; Lerdahl & Jackendoff, 1983). Most of these theories suggest that segmentation (a process which underlines the organization of musical events into groups) is a fundamental aspect for the creation of a long-term representation (Deliège, 1987).

A novel theory of brain function which has relevance also for music perception and memory studies is predictive coding theory (PCT), a Bayesian mathematical model of neural mechanisms initially used for visual perception (Rao & Ballard, 1999) and subsequently used to the prediction of behavior (Fitzgerald, Dolan & Friston, 2014). PCT concerns the hierarchical neuroarchitecture that allows and makes sense of the external or internal environment. When applied to music, PCT represents an attempt to understand how the human brain predicts, understands and memorizes sounds.

Predictive coding is based on the bidirectional flow of information in a hierarchical neural network (Friston, Stephan, Montague & Dolan, 2014), and, applying it to auditory perception, postulates how the succession of sounds is recorded and compared with pre-existing models which, if these sounds do not correspond to the models, are updated from time to time (for a review, cfr. Koelsch, Vuust & Friston, 2019). The higher representation units send their predictions to the lower units. The bottom-up input is compared with these top-down predictions and if there is a match between the input and the prediction, a suppressed neural response (which corresponds to the passive sensory adaptation mechanism) is obtained. Conversely, a mismatch causes a prediction error response, measured with electroencephalography or magnetoencephalography as the mismatch negativity (MMN), which is projected back to the higher level (Kanai *et al.*, 2015). These neurological processes driving optimum deviant identification fluctuate according to gene-determined catecholamine levels in the brain, according to Bonetti *et al.* (2021a). As Vuust *et al.* (2022) state, a key concept in PCT is the idea that prediction mistakes are weighted by their precision (predictability). In other words, the brain must choose the prediction errors that drive Bayesian belief updating and the top-down predictions that follow. This can be thought of as a type of covert or mental action that gives ordinary predictive coding systems an active and attentional component. These theoretical models have mainly sought empirical confirmation in locationist research, including studies focused on the MMN brain response, which will be illustrated in the following section.

Locationist research on the neural bases of sensory memory for musical sounds

A deep understanding of non-verbal, and specifically, musical auditory memory requires the identification of its neural substrates and the mechanisms involved. For this purpose, the research with neuroimaging methods is crucial, as also highlighted in the most recent manuals of general psychology and memory (e.g., Baddeley, Eysenck & Anderson, 2020; Gatti & Vecchi, 2021). It should be noted, however, that neuroscience and neuroimaging studies have focused too mainly on the coding and recognition of visual, spatial (Aggleton & Brown, 2006; DiCarlo, Zoccolan & Rust, 2012) and verbal information than auditory ones. In the following sections we will review the few studies in the literature on the neural correlates of memory for musical sounds, starting from systemic neuroimaging studies, then moving on to neurophysiology studies to conclude with studies on dynamic functional connectivity.

In the sensory span, predictive processes, traditionally referred to as echoic memory processes, rely on interconnected neural structures that go from the peripheral to the central nervous system, namely the acoustic nerve, the primary and associative auditory cortex, the superior temporal gyrus, the insula and the inferior frontal gyrus (Kanai *et al.*, 2015; Näätänen *et al.*, 2001; Tervaniemi & Hugdahl, 2003; Zatorre, 2003).

Neurophysiological research has demonstrated the coexistence of different mechanisms for coding and storing simple sound sequences by activating the aforementioned brain areas. The neurophysiological responses at the level of the auditory cortex adapt and attenuate with the repetition of tones in a sequence, at least until a new tone is introduced, as occurs with the oddball paradigm. This dampening of neuronal response related to forming predictions and the opposite enhancement related to signaling a change or error in expectation are studied by recording the mismatch negativity (MMN) and the N1 or N100, two kinds of brain responses evoked by stimuli, by means of EEG and MEG (Brattico, Näätänen & Tervaniemi, 2001; Brattico, Tervaniemi & Picton, 2003; Brattico *et al.*, 2009; Näätänen, Gaillard, & Mäntysalo, 1978; Näätänen *et al.*, 2007; Vuust *et al.*, 2011; Vuust *et al.*,, 2012). MMN reflects the formation of a neural representation of standard sound to which the deviant sound is related (Näätänen & Winkler, 1999): without this standard predictive sound encoding, no MMN could be generated (Cowan *et al.*, 1993). MMN is generated both in the primary auditory cortex (Alho *et al.*, 1986; Hari *et al.*, 1984; Kropotov *et al.*, 1995; Sams *et al.*, 1985) and in the frontal lobe after the attention switching that follows the stimuli changing, as proposed by Näätänen and Michie (1979) and then confirmed by various studies (e.g., Giard *et al.*, 1990; Rinne *et al.*, 2000).

Using a multi-feature MMN paradigm, Kliuchko *et al.* (2019) discovered that active listening experience in professional musicians enhances neuronal prediction errors above and beyond the effect of just listening to music. In particular, they observed larger MMN amplitudes, indicating a stronger brain response to violated priors, in jazz musicians (but not in classical musicians) as compared to non-musicians or amateurs. Participants who were not musicians but who loved jazz music, instead, showed a reduced MMN to pitch slide (a common feature in jazz music). These results suggest that priors learned from active vs. passive engagement with a musical style shape the auditory-cortex responses to deviations of spectral features (such as timbre, pitch and slide) inserted in an ever-changing fast musical sequence. For example, professional jazz musicians display a more accurate neural discrimination of pitch, pitch slide, timbre and intensity changes, as indexed by the MMN response. Furthermore, a higher preference for a musical style in non-musicians or amateurs was associated with a reduced MMN response to pitch slide, which is the opposite to the effect of music playing experience in the same population. This suggests that active experience of a musical style is crucial for developing accurate priors and consequently an enhanced automatic neural discrimination of the sound features of the preferred style, in contrast to a passive experience of it (Kliuchko *et al.*, 2019).

Thanks to the MMN it was discovered that the human brain is more efficient in discriminating frequency changes between sounds if the sound spectrum is complex. In particular, Tervaniemi *et al.* (1993) have discovered that the MMN amplitude to the same amount of frequency changes increases, and the latency is reduced while using piano sounds compared to simple (sinusoidal) tones. Along the same line, Tervaniemi *et al.* (1997) have demonstrated how pitch changes were detected more accurately and evoked a larger MMN with a shorter latency when sounds had a richer spectrum than with sinusoidal tones. Hari *et al.* (1992) compared MMNm (that is the magnetic equivalent of the electric MMN) in response to frequency changes of isolated sinusoidal tones with that to changes within paired tones, discovering a stronger MMNm in the latter case. According to the authors, these results demonstrate that the strength of memory traces depends on the complexity of the stimuli.

MMN can be generated by two distinct mechanisms: the first is called “passive sensory adaptation” or “neuronal refractoriness” to individual tones and occurs after prolonged exposure to repetition of stimuli or sound features (Brattico *et al.*, 2003). The second one is the «predictive coding based on the probability of transition between tones» (Dehaene *et al.*, 2015). Therefore, from the studies listed above it emerged that brain anticipates better the errors in the case of complex sounds, but it was also seen how this ability is more evident in musicians than in nonmusicians (Brattico *et al.*, 2009; Koelsch, Schröger & Tervaniemi, 1999; Vuust *et al.*, 2012). In a similar way, Brattico *et al.* (2001) reported a shorter left-lateralized MMN latency to familiar tone patterns than unfamiliar ones, suggesting that musicians have faster neural mechanisms in the left hemisphere to process pitch pattern changes, probably thanks to daily musical training with that type of sound material. Further studies have been then conducted: Tervaniemi, Huotilainen & Brattico (2014) found that when folk musicians were compared to non-musicians, the MMN was larger for mistuned sounds, possibly as a consequence to the central role of melody and pitch in Finnish folk music. Furthermore, Quiroga-Martinez *et al.* (2019) discovered that high-entropy stimuli, consisting of a set of non-repetitive melodies, had lower MMNm amplitudes for pitch and slide deviants than low-entropy (LE) stimuli, consisting of a simple, repetitive pitch pattern. These findings are consistent with predictive coding theories (Clark, 2013; Feldman & Friston, 2010; Hohwy, 2012) and models of musical expectations (Hansen, Dietz & Vuust, 2017; Ross & Hansen, 2016; Vuust *et al.*, 2018) which propose that prediction error responses are reduced in contexts with low as compared to high predictive precision. This study confirms that precision of auditory (musical) models affect prediction error while listening.

In sum, MMN studies demonstrated neural mechanisms for sensory predictions of music in the short-term, as affected also by long-term experience and second-order predictions, helping us to understand how the human brain processes auditory information from the environment.

Working memory for music and its neural correlates

Few recent fMRI studies using verbal and non-verbal auditory stimuli have revealed that WM for sounds activates areas such as the frontotemporal gyrus, the supramarginal regions and the cerebellum (Gaab *et al.*, 2003). An fMRI study by Schulze *et al.* (2011) investigated the neuroanatomical correlates of verbal and musical WM in relation to music training and found that WM-related neural structures namely the Broca's area, motor and premotor areas, the left insular cortex and the inferior parietal lobe, were activated for both verbal and tonal n-back tasks, with no significant differences between musicians and non-musicians. Furthermore, specific areas were activated in the musicians' brains either only during verbal n-back tasks (right insular cortex) or only during tonal n-back tasks (right globus pallidus, right caudate nucleus and left cerebellar hemisphere). These findings suggest the existence of two WM systems in musicians: a phonological loop and a tonal loop (Schulze *et al.*, 2011).

Pallesen *et al.* (2010) measured the metabolic activity of the brain (blood-oxygen level dependent or BOLD signal) in musicians and nonmusicians during an n-back task with musical chords transposed over several octaves in order to determine the relationship among performance, musical proficiency, and overall enhanced cognition. From this study it emerged that musicians had a better performance in WM tasks than nonmusicians, and as WM load increased, musicians demonstrated higher increases in BOLD brain responses than non-musicians, replicating the well-known association between WM load and task performance (Baddeley, 1986; Just & Carpenter, 1992; Sternberg, 1969). The study also suggests that superior WM task performance in musicians rely on an enhanced ability to exert sustained cognitive control, which may be a consequence of focused musical training. Furthermore, Salmi *et al.* (2010), using the same dataset as Pallesen *et al.* (2010) demonstrated that this load increase in a musical WM task is associated with enhanced brain activity in the parietal, dorsal premotor, and lateral prefrontal cortices as well as lobules VII–VIII of the posterior cerebellum, while on the contrary the 0-back sensory-motor task activated the motor/somatosensory, medial prefrontal, and posterior cingulate cortices and lobules V/ VI of the anterior cerebellum, suggesting that the posterior cerebellar activation during a demanding cognitive task is involved with optimization of the response speed.

In the studies mentioned above, WM was studied using controlled button-press tasks with simple musical stimuli, that likely generate mental states that are different from those emerging from real-life listening situations. To overcome this limitation, Burunat *et al.* introduced the naturalistic paradigm in musical memory studies by means of fMRI (Burunat *et al.*, 2014). Two different experiments were conducted within the same study. A first experiment was a listening test with musicians and amateurs and the piece “Adios Nonino” by Astor Piazzolla. This experiment was functional to identify segments of the piece that were used as regressors for the analysis of an fMRI experiment, in which a separate group of musicians listened freely and attentively to the same musical piece without any interruptions. The statistical maps of the t-tests between the repetition of the motifs and their first presentations showed activations of brain regions related to WM for the musical motifs: hippocampus, basal ganglia, dorsolateral prefrontal cortex (PFC) and cerebellum (Figure 1). These results not only replicated previous studies on musical WM where artificial sequences or isolated chord cadences were presented to the participants but highlighted the role of the hippocampus, never clearly found in a musical memory neuroimaging experiment. No activations of the supratemporal auditory regions emerged since sensory coding processes were excluded from the main analyses by using covariates.

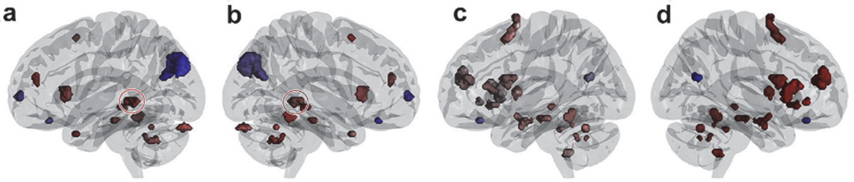

Figure 1. Left and right lateral ([a] [d]) and mid-sagittal ([b] [c]) views of the thresholded statistical map displaying positive (red) and negative (blue) correlations with the WM regressor. The hippocampal activation is indicated in the left hemisphere. Figure reproduced with permission by Burunat *et al.* (2014). Dynamics of brain activity underlying working memory for music in a naturalistic condition. *Cortex*, 57, 254-269. Copyright Elsevier.

Further studies using the naturalistic free-listening paradigm were conducted also with MEG and EEG methods. These studies were aimed at extracting transient evoked cortical responses to musical features during realistic listening. Haumann *et al.* (2021) discovered that naturalistic P1/N1/P2 transient evoked cortical responses (ERs) can be extracted with high reliability at sound onsets in real musical pieces, and that naturalistic P2 responses are localized to core cortical regions of the auditory cortex. P1/P2 responses were shown to be predominant in monophonic/homophonic passages of the music (piano solos), whereas N1 responses were only detectable in the polyphonic parts with the whole orchestration. The authors observed that the P2 responses were evoked by increases in the acoustic features of intensity and spectral flux, which are commonly used to locate the onset times of syllables in speech and the onsets of tones in musical pieces (Alías *et al.*, 2016). This result can be interpreted according to many theories, such as predictive coding but also superposition, refractoriness or habituation (Heilbron & Chait, 2018). Predictive coding theory may explain the lack of measurable early brain responses to repeated stimuli (Bendixen, Schröger, & Winkler, 2009; Brattico, Bogert & Jacobsen, 2013; Herrmann *et al.*, 2015; Todorovic *et al.*, 2011; Vuust *et al.*, 2009; Winkler, Denham & Nelken, 2009), as well as the hypothesis of stimulus-specific habituation and dishabituation (Butler, 1968, 1972a, 1972b; Fruhstorfer, Soveri & Järvilehto, 1970; Graham, 1973; Gu *et al.*, 2018; Loveless, 1983; Megela & Teyler, 1979; Näätänen & Picton, 1987; Näätänen *et al.*, 1988; Öhman & Lader, 1977; Picton *et al.*, 1978; Thompson & Spencer, 1966; Thompson & Groves, 1973; Woods & Elmasian, 1986). The superposition hypothesis focuses on overlapping cortical responses in M/EEG waveforms, which are commonly observed in fast rate events (Simon, Balla, & Winkler, 2019; Tan *et al.*, 2015), so the sum of the overlapping response waveforms will result in cancellation or summation between the overlapping positive and negative evoked potentials or fields. The observed lower (or higher) response amplitudes might be accounted for by this destructive (or constructive) interference. However, it has been noticed that the superposition hypothesis is insufficient for characterizing additional amplitude changes across inter-onset intervals stimuli (IOI) in studies where fast steady-state responses (SSR, with periodic stimulation greater than 1 Hz) have been simulated by increasing the rate of overlapping cortical ERs (P1/N1/P2) (Tan *et al.*, 2015). SSR phenomenon supports the theory of "stimulus-specific entrainment" posing that the spontaneous cortical oscillations of neuronal assemblies lock to the environmental stimuli modulating power of oscillations according to the exogenous frequencies (e.g., Brenner *et al.*, 2009).

A further explanation of cortical memory processes is represented by the cortical refractoriness theory, stating that over a ten-second recovery time, a group of stimulated cortical neurons reacting to a stimulus becomes less receptive (Brattico *et al.*, 2003; Zacharias, König, & Heil, 2012). This "passive adaptation effect", also known as "neural fatigue", is thought to be a mechanism that "boosts sensory systems" processing efficiency (Grill-Spector, Henson, & Martin, 2006). The excitability of cortical neurons is progressively restored throughout this recovery phase. The auditory cortex neurons have a shorter time to fully recover their excitability when the sound elements of interest are presented with shorter IOIs. As a result, cortical excitability would be reduced, as would the amplitudes of cortical ERs. Nonetheless, the cortical refractoriness theory has been questioned by new findings indicating the role of expectancies (or "predictions") (Costa-Faidella *et* *al.*, 2011; Euler & Ricci, 1958; Pearce *et al.*, 2010; Serkov, Leonova & Shelest, 1969; Todorovic *et al.*, 2011).

Long term musical memory and its neural correlates

Numerous studies have tried to investigate musical LTM in Alzheimer's disease (AD), a type of dementia that primarily affects memory, thinking and behavior, to evaluate residual abilities. For instance, Lola Cuddy's studies suggest that some sort of LTM for music is preserved in most cases of AD patients (Vanstone & Cuddy, 2009). Further studies have made it possible to advance the hypothesis that explicit musical memory is impaired in most AD cases, supporting the notion that the brain regions most affected since the early AD stages – particularly the frontal lobe – mediate this kind of memory. What seems to be preserved is implicit memory, which in musicians corresponds to the procedural memory of playing an instrument, suggesting how AD does not fully compromise these brain functions and supporting the distinction between explicit and implicit musical memory (Baird & Samson, 2009). Moreover, music has been demonstrated to facilitate autobiographical memories in AD patients (Peck *et al.*, 2016). In particular, Irish and colleagues (2006) discovered that total autobiographical recall was considerably better in the music than in the silent condition when comparing the influence of background music against a silent testing condition on autobiographical memory in people with moderate Alzheimer's disease. Furthermore, García *et al.* (2012) presented samples from several kinds of music, including joyful music, sad music, new music, and industrial noise, to see if the observed benefits in autobiographical memory in AD patients are music-specific. When compared to all other conditions, autobiographical memory was considerably improved when exposed to sad music, but only for recall of remote memories and not for recent memories. The authors propose that it is not the music itself that enhances remote autobiographical memory recall, but rather the emotion that goes along with it, and that the ability of music to specifically promote recall of distant rather than recent autobiographical memories may be significant in restoring a sense of identity. These findings have then been confirmed by another study by Cuddy *et al.* (2017), showing that the presence of song lyrics or even favorite music is not required to elicit autobiographical memories; rather, “pure” instrumental music that is widely known in the culture is sufficient. Regardless of this, listening to favorite music elicits a specific activation of the supplementary motor area, which has been linked to memory for familiar music and is often spared in early AD (King *et al.*, 2019). Following the presentation of preferred musical stimuli, King and colleagues discovered widespread increases in functional connectivity in corticocortical and corticocerebellar networks, indicating a transient impact on brain function and supporting a mechanism through which attentional network activation in the brain’s salience network improves brain network synchronization.

Another study by Johnson *et al.* (2011) propose to compare music recognition in a clinical population with various types of dementia (i.e., AD, frontotemporal and semantic dementia), and results have shown how patients with semantic dementia had considerable difficulty naming familiar melodies and also scored the lowest when asked to identify pitch errors in the same melodies, suggesting that naming familiar melodies is strongly related to measures of semantic memory. After that, voxel-based morphometry analysis of AD brains revealed that an impairment in naming songs was linked to the bilateral temporal lobes and inferior frontal gyrus, whereas difficulty detecting pitch errors in familiar melodies was linked to alterations in the right temporal lobe. These findings suggest that the anterior temporal lobes are involved in the memory system for melodies, and that musical functions are impacted differently in different types of dementia.

More recently, further studies have been conducted to better investigate the role of different areas for the recognition of complex musical patterns: for this purpose, Bonetti *et al.* (2021b) combined MEG and MRI, discovering a dual processing brain mechanism. The single tones forming the patterns were independently elaborated by a rapid, oscillatory, local processing driven by the auditory cortex. The combination of those single tones into a meaningful superordinate pattern, instead, seems to depend on a simultaneous global, slow processing that also involves a widespread network of sequentially active high-order brain areas largely related to audition, memory, attention and decision-making, i.e., the hippocampus, cingulate gyrus, inferior temporal cortex, frontal operculum, insula (Bonetti *et al.*, 2021b).

In another MEG study (Fernández-Rubio *et al.*, 2022), 71 participants first listened for a few times to a prelude in C major by J. S. Bach as well as to an acoustically and structurally matched atonal piece and then had to recognize if 5-tones patterns were previously heard or not (old/new task). Results showed that the superior behavioral recognition for tonal patterns that were previously heard and memorized was supported by memory-related brain areas such as the left hippocampus and cingulate. In turn, the worse recognition of atonal patterns activated only an auditory temporal network. Due to its binding function, the hippocampus involved in recognition memory for tonal sounds might be related to a wide range of situations involving auditory information, such as integrating acoustic features into a perceptual whole, anticipating the continuation of sound sequences, and "mental navigation" along sequences of auditory stimuli (Billig *et al.*, 2022).

From locationism to the static connectome

In the search for the neural basis of memory, studies in the field of neuropsychology, with brain-damaged patients, and neuroimaging, with fMRI, have allowed to isolate the contribution of each brain region, albeit at a low temporal resolution, since the fMRI signal summarizes the BOLD signal over the course of a few seconds. A better temporal resolution useful to studying the unfolding of auditory memory traces following one another at a very fast rate can be obtained with neurophysiological techniques such as EEG and MEG. Although these techniques have a very detailed temporal resolution, at a spatial level the source reconstruction of the neural sources originating the MEG/EEG responses to sounds are typically limited to regional activity, and specifically often only to the bilateral auditory cortex. Hence, these studies can be described as "locationists" for their intent to map memory functions in specific structures of the central nervous system. In the last decade, the locationism approach has been complemented by a novel, dynamic approach that shows the synchronous interaction of various brain structures for the formation and codification of sound memories, as will be illustrated later. However, the analysis of single brain regions provides an incomplete picture of brain functions and mechanisms.

The latest viewpoint balances integration and segregation, conceiving the relation between structure and function as based on dynamic communication among brain areas, hence emphasizing the need for imaging the fiber tracts and for computing correlations between neural responses from different locations of the brain in, respectively, structural or functional connectivity (FC) studies (Sporns, 2012). Structural connectivity among brain regions seeks physical connection networks in the brain. In turn, static FC highlights activation similarities between brain regions regardless of the anatomical connections between them.

According to the FC approach, the interactions between circuits and regions of the brain are examined, quantifying whether the fluctuations in neuronal activity originating from each region are correlated over time. The frequencies at which these fluctuations have the greatest power during WM tasks are between 4 and 8 Hz, especially in the hippocampus and prefrontal regions (Tesche & Karhu, 2000). In the study by Burunat *et al.* (2014), a PPI (Psychophysiological Interactions) analysis was conducted, revealing not only the modulatory effects of WM on FC patterns, but also how most of the areas relevant to WM (left hippocampus, putamen right, right caudate nucleus and right frontal gyrus) seem to function independently during WM tasks, possessing intrinsic FC related to listening to motifs that has been already presented. Neural connections related to musical memory have been measured even in the brain of babies in two recent studies (Lordier *et al.*, 2019; Loukas *et al.*, 2022). By comparing the resting brain activity of infants who had listened to familiar music for ten minutes a day, for several weeks, an intrinsic static FC was found between regions of the auditory cortex, and then between orbitofrontal cortex and motor regions, as well as between amygdala and thalamus in the right hemisphere, therefore, between areas linked to the encoding of emotional memories.

From static to dynamic connectivity: the temporal evolution of brain memory networks

Advanced analytical methods can measure the "effective connectivity", which quantifies the causal influence of one area over another, as well as how connectivity varies based on task variables (Buckner, Krienen & Yeo, 2013; Fornito & Bullmore, 2012). In a study conducted by Lumaca *et al.* (2021), for example, effective connectivity was measured during the learning of complex tone patterns using dynamic causal modeling on fMRI data. The results of the study showed a decrease in inhibitory connectivity within left Heschl's gyrus and an increase in feedforward connectivity from the left Heschl's gyrus to planum temporale during the presentation of deviant stimuli, suggesting that complex auditory prediction errors are encoded by changes in feedforward and intrinsic connections, confined to the superior temporal gyrus).

Effective connectivity as well as static FC, however, provide only a snapshot of the brain processes related to a task. When a task evolves over time, as in the case of music, it becomes necessary to adopt a dynamic approach, which allows the evaluation of the passage of information through the various neural systems, from coding to retention and recovery, in a dynamic process that develops temporally.

In the last few years, a totally new approach called "dynamic connectome" has emerged. This approach derives from the observation made by scientists who have found how the FC networks changed significantly according to the brain state of the participants, such as sleep, mental tasks and learning, and even during the course of the same experimental session, correlating with the behavior (for a review, cfr. Leopold & Maier, 2012). Thanks to the work of scientists like Olaf Sporns, Danielle Bassett, Edward Bullmore, Gustavo Deco and Morten Kringelbach, methods of physics of complex networks have been introduced in cognitive neuroscience to analyze changes in the FC, giving rise to the new approach called «dynamic functional connectivity» (DFC).

By DFC we refer to the phenomenon according to which FC changes in a short period, and it is a recent expansion of traditional FC analysis which generally assumes that functional networks are static over time (Allen *et al.*, 2014; Calhoun *et al.*, 2014; Hutchison *et al.*, 2013; Sakoğlu *et al.*, 2010). It has recently been suggested that DFC is a more accurate representation of functional brain networks, which evidences in a better way neurological and psychiatric disorders than static FC (Zhao *et al.*, 2020). The main instrument to measure DFC is the fMRI. Nevertheless, fMRI measures metabolic changes of the BOLD signal in a very different time scale compared to the electrophysiological measurements of neural synchrony obtained on animal models, or with EEG or ECoG (electrocorticography) on humans. Therefore, due to the slow time course of the BOLD signal, the FC resulting from fMRI can only quantify the correlations that occur at frequencies below 0.1 Hz (Fox & Raichle, 2007), allowing to partially highlight the temporal development of a complex dynamic process such as that related to auditory memory. On the other hand, electrophysiological recordings typically measure synchrony at frequencies between 1 and 100 Hz, and for this reason DFC studies on the MEG signal have been published in recent years (Bonetti *et al.*, 2020; Bonetti *et al.*, 2021c; Bruzzone *et al.*, 2022).

To obtain DFC from signals that are fMRI or MEG, the "correlation-based sliding window" analysis is usually used (for a review, cfr. Preti *et al.*, 2017), which was introduced for the first time by Sakoğlu *et al.* (2010) in a schizophrenia study. This approach consists in correlating fMRI signals between distinct brain regions with a predefined number of time points that form a "window". This defined window is then moved a certain number of scans forward in time and then an additional analysis is performed, which reflects the presumed temporal changes associated with the spontaneous activity of brain networks. Another and more recent approach is Instantaneous Phase Synchrony (IPS; Omidvarnia *et al.*, 2016), which compares the phase angles for each voxel or brain region (depending on the area of interest) at each individual time point, thus providing the same temporal resolution as the original fMRI data.

For the first time, the dynamics of the formation of memory traces and of the recognition of musical sounds through DFC have been studied during the recall of sound patterns learned during the experimental session (Bonetti *et al.*, 2020). The sample of 70 participants, made up of musicians and non-musicians, was required to listen carefully for 10 minutes of the Prelude in C minor BWV 847 by J. S. Bach. During a subsequent MEG measurement, an excerpt from the Prelude they had previously listened to, or a new variation pattern also by Bach, were presented to the participants. Aim of the study was to find the brain sources of the differences between the condition in which the Bach pattern was recognized and the conditions in which the new variation occurred, by calculating the dynamic brain connectivity between all neocortical regions. From DFC analysis, it emerged that the hippocampus, the cingulate gyrus and the PFC are more connected to the rest of the brain when the incoming stimuli correspond to the prediction (Bach original), while the auditory cortex appears more central (mainly connected with the motor cortex and dorsolateral PFC) to indicate the violation compared to prediction (while listening to the Bach variation).

Hence, the novel DFC approach adopted in the study by Bonetti *et al.* (2020) allowed to examine not only the previously-observed hippocampal and frontal involvement in musical memory but also the involvement of brain structures such as the insula, frontal operculum and basal ganglia, which play a role both in the classification of salience of the stimuli and in the detection of prediction errors during listening (Cauda *et al.*, 2011; Limongi *et al.*, 2013; Uddin, 2015).

Conclusion

To summarize, we argue that the recent technical developments allow us to move away from a locationist approach towards understanding the dynamic organization of the fast-changing connections between brain areas during the various memory stages: from encoding to consolidation and recall. As Bassett and colelagues pointed out (2011), learning and memory require “rapid adaptation to an ever-changing environment”. Only neuroimaging methods that consider the dynamics of brain activity and connectivity will be effective in describing learning and memory in relation to an ever-changing, complex environmental stimulus such as music.

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