REVIEW

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Swinging in the brain: shared neural substrates for behaviors related to sequencing and music

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Music consists of precisely patterned sequences of both movement and sound that engage the mind in a multitude of experiences. We move in response to music and we move in order to make music. Because of the intimate coupling between perception and action, music provides a panoramic window through which we can examine the neural organization of complex behaviors that are at the core of human nature. Although the cognitive neuroscience of music is still in its infancy, a considerable behavioral and neuroimaging literature has amassed that pertains to neural mechanisms that underlie musical experience. Here we review neuroimaging studies of explicit sequence learning and temporal production—findings that ultimately lay the groundwork for understanding how more complex musical sequences are represented and produced by the brain. These studies are also brought into an existing framework concerning the interaction of attention and time-keeping mechanisms in perceiving complex patterns of information that are distributed in time, such as those that occur in music.

Music might be thought of as the artful patterning of acoustic information according to rules and conventions that specify different genres and styles. As such, music is a sensory phenomenon that elicits perceptual and emotional responses. These responses shape our minds' journeys through musical space. Further reflection suggests, however, that music is as much about action as it is about perception. Simply, music moves us. When music engages the human mind most strongly—when performers play music, or when listeners tap, dance, or sing along with music—the sensory experience of musical patterns is intimately coupled with action. Thus, music is an excellent example of a 'perception-action cycle' and may serve as a model system for understanding neural circuits and mechanisms engaged in sensorimotor coupling. This model offers a view of the brain in which perceptual and motor systems are coupled across multiple levels of processing[1,2]. Relatively simple coupling might be foot-tapping in synchrony with the perceived beat in a piece of music, whereas more complex coupling would be dancing a waltz, singing a song, or playing a melody on a violin.

How and where in the brain is the coupling of the perception and production of sequences of varying complexity achieved? Here we address this question by examining evidence that is particularly relevant to music: studies of sequence learning and of sensorimotor coordination during tapping tasks. The goal of this review is twofold: to consider the results of behavioral and neuroimaging studies of sequence learning and timing in the context of music, and to identify points of overlap with behavioral and neuroimaging studies of music cognition.

The cognitive psychology of sequence perception and production

Music can be thought of as sequences of events that are patterned in time and 'feature space'. The feature space is multidimensional and consists of both motor and sensory information. Motor patterns determine how we position effectors in space, such as fingers on piano keys, at the appropriate times to generate specific melodies, chords and rhythms. Sensory patterns reflect the organization of auditory objects, such as notes or sets of notes played by specific instruments, in time. Rhythm describes the temporal and accentual patterns that are associated with the actual sensory or motor events. In the case of the performer, action and perception sequences are tightly coupled because the goal of specific actions is to produce specific sounds at appropriate times, often in response to antecedent events. Three research domains in psychology and neuroscience—timing, attention and sequence learning—are particularly pertinent to understanding the neural basis for sequencing behaviors in music.

Timing

Music incorporates a variety of temporal patterns. These may be isochronous sequences in which temporal intervals are of a single, constant duration, or, more commonly, polyrhythmic sequences containing temporal intervals of different durations. The ability to synchronize with sensory information is necessary for playing in an ensemble, and the ability to maintain an internal tempo is necessary in any solo performance. What are the timing mechanisms by which these sequences are effected under externally and internally paced conditions? Numerous studies have examined how subjects synchronize taps with a pacing signal, continue tapping at the rate of the pacing signal, or tap out-of-phase with a pacing signal (syncopation). Others have examined multi-limb coordination in the production of

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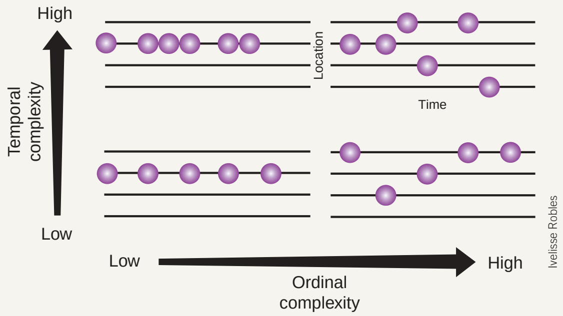
Box 1

Music we encounter (and sequences in general) range widely in both temporal and ordinal complexity. In this illustration, each circle denotes the time of a finger movement, and each vertical line signifies a spatial location or finger that is to be tapped or moved (or could represent a musical note). The sequence of lowest temporal and ordinal complexity is produced with a single effector, and the timing between events is constant. Mixing intervals with different durations in the sequence increases temporal complexity; ordinal complexity is increased by adding new spatial locations or notes (or by increasing the length of a sequence). See **Supplementary Audio 1–4** online.



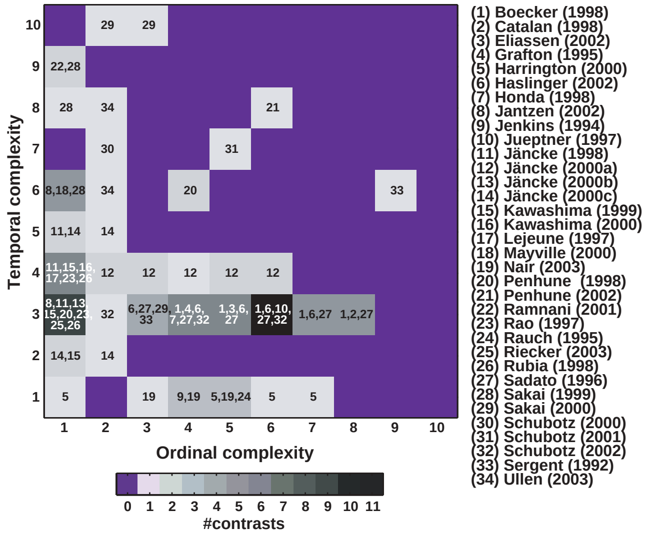
rhythms. The basal ganglia and the cerebellum are thought to have important roles in timing, but the question of whether perception and action are timed with reference to neural populations that are dedicated to timing distinct intervals, or whether maintaining temporal precision in perception and action is an emergent property of a dynamical system, is still a matter of considerable debate[3–6].

Given the uncertain nature of clock mechanisms underlying mental timekeeping, musical behaviors provide important insights into basic properties of these timekeeping mechanisms. For example, it has been observed that sequences in which the durations of intervals are in ratios of simple integers, such as those that typically occur in music (1:2, 1:3 or 1:2:3), are easier to remember and reproduce than other sequences in which the metrical properties do not conform to simple integer ratios. This finding led to the hypothesis that simple-ratio rhythms are able to induce internal clocks that then facilitate the perception and production of metrically related time intervals, whereas non-metrical intervals require an explicit memory of each interval encountered in a given sequence[7,8]. More generally, it is postulated that the rhythmic properties of a piece of music entrain neural oscillators that facilitate synchronization of both perception and action with the underlying beat in music[9,10].

Recent behavioral studies using synchronization tapping in conjunction with timing manipulations of musical stimuli have provided additional insights into the brain's timekeeping processes. Perception and action are tightly coupled during synchronization tapping, as evidenced by automatic timing adjustments to subliminal perturbations[11,12] and the need for continued sensory information for phase correction[13]. However, introducing timing variability into a piece of music, as would occur during any expressive performance, negatively impacts the perceptual ability to detect temporal deviations from isochrony in a subsequently presented sequence, even though motor variability in synchronization tapping during the subsequent sequence is unaffected. This result suggests the presence of multiple and somewhat independent timing mechanisms involved in conscious perception of temporal variability and regulation of action[14]. Intriguingly, the structure of a piece of music, or the accent structure in a click sequence, introduces predictable deviations into timing mechanisms underlying both perception and action, suggesting that timing processes are adjusted dynamically[12,15,16].

Sequencing

Sequences of time intervals are necessarily accompanied by sequences of perceptual or motor events, and these conjunctions are of particular importance in music. One of the most widely used tasks for studying how the brain represents and learns event sequences is the serial reaction-time (SRT) task[17]. In a standard 'spatial' version of the SRT task, an item appears at one of several positions on a screen, and subjects must respond as quickly as possible by pressing a button corresponding to the stimulus location. After a brief interval, the next item appears, a response is made, and so on. As the SRT task proceeds, response times get shorter if the sequence follows a repeating pattern, indicating that subjects form expectations about the stimulus location and/or motor response. SRT learning bears some similarity to learning how to play a melody on an instrument or to sing a song, in that a motor program is executed in response to a visual or auditory cue, or to a memorized representation of a longer sequence. In contrast to learning a musical sequence, in which it is necessary to execute the correct movement at the correct time, responses to cues in the SRT are made as quickly possible. Thus, SRT learning occurs outside of a regular temporal context.



(1) Boecker (1998)
(2) Catalan (1998)
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(11) Jäncke (1998)
(12) Jäncke (2000a)
(13) Jäncke (2000b)
(14) Jäncke (2000c)
(15) Kawashima (1999)
(16) Kawashima (2000)
(17) Lejeune (1997)
(18) Mayville (2000)
(19) Nair (2003)
(20) Penhune (1998)
(21) Penhune (2002)
(22) Ramnani (2001)
(23) Rao (1997)
(24) Rauch (1995)
(25) Riecker (2003)
(26) Rubia (1998)
(27) Sadato (1996)
(28) Sakai (1999)
(29) Sakai (2000)
(30) Schubotz (2000)
(31) Schubotz (2001)
(32) Schubotz (2002)
(33) Sergent (1992)
(34) Ullen (2003)

Figure 1 Summary of the complexity of behavioral tasks examined in 34 neuroimaging studies of sequence learning and/or time-interval production. Ordinal complexity represents the number of items in a sequence and/or the number of fingers and limbs that are involved in the task. A score of 1 represents a tapping task involving a single finger. A score of 5 represents 8-item sequences that are produced with 4 fingers, but in which the sequence information is restricted to a single dimension, such as spatial location. A score of 10 would be assigned to conditions of bimanual coordination in extended sequences of more than 20 items coded along multiple feature dimensions, such as spatial location and pitch. Along the dimension of temporal complexity, 1 refers to conditions in which the requirement is to produce finger sequences as fast as possible. A score of 2 indicates conditions of self-paced isochronous tapping; a score of 3 indicates isochronous timing with interstimulus intervals shorter than 2 s; a score of 6 indicates time-intervals that comprise simple integer ratios, such as 1:2 or 1:2:4; scores 7–8 reflect polyrhythmy using more complex integer ratios such as 1:3 or 2:3; and scores 9–10 reflect temporal complexity that is rarely encountered in music: non-integer ratios or random time intervals that form non-integer ratios. See **Supplementary Note** online for additional information about this figure and the list of citations.

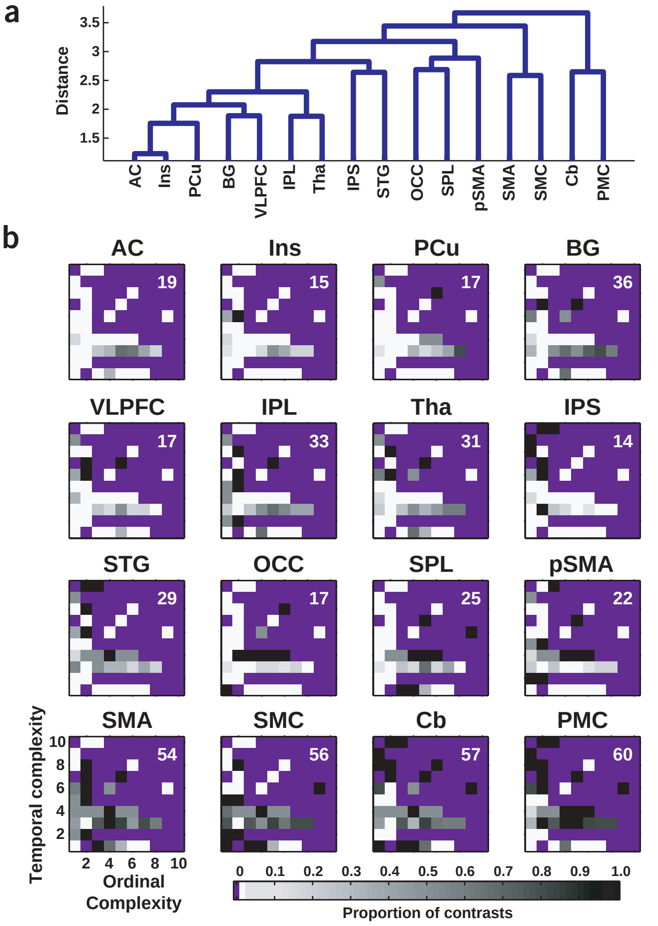

Figure 2 Patterns of responsiveness of different brain areas across levels of temporal and ordinal complexity. For each brain region reported as an activation locus in the studies summarized in **Fig. 1**, we tallied the number of times that brain region was reported for a contrast falling at each location on the complexity grid. These totals were then normalized by dividing by the values in **Fig. 1** to obtain the proportion of possible times the region was reported to be activated by a contrast of particular temporal and ordinal complexity. Thus, each brain area was associated with a complexity pattern. (**a**) Cluster analysis of complexity patterns. In order to identify common complexity patterns across brain regions, the normalized complexity patterns for these 16 regions were clustered using a hierarchical clustering algorithm. Related patterns are connected to a common node, and the height of the node reflects the distance between the patterns. (**b**) Proportion of contrasts in which brain regions are observed to be active at different combinations of temporal and ordinal complexity. The number of entries in the complexity grid for each brain area is shown in the top-right corner of each grid. Regions of missing data are shown in magenta. Abbreviations: AC, anterior cingulate; Ins, insula; PCu, precuneus; BG, basal ganglia; VLPFC, ventrolateral prefrontal cortex (from frontal operculum to just below inferior frontal sulcus); IPL, inferior parietal lobule; Tha, thalamus; IPS, intraparietal sulcus; STG, superior temporal gyrus; OCC, occipital cortex; SPL, superior parietal lobule; SMA, supplementary motor area; pSMA, pre-SMA; SMC, sensorimotor cortex; Cb, cerebellum; PMC, premotor cortex. See **Supplementary Note** online for additional information about this figure.

In music, spatial and temporal sequence information must be unified. There is evidence that unified spatial and temporal representations arise in the SRT task: spatial sequence learning is facilitated when accompanied by a patterned temporal sequence, even if subjects are not instructed to learn the temporal sequence, or even when they are unaware of it[18]. More generally, the interactions of temporal and tonal sequences can be thought of in terms of a joint-accent structure that specifies conjunctions of rhythmic and melodic events[19]. The accent structure of music shapes both temporal and tonal, or melodic and harmonic, expectancies (what will happen when)[20–22], and it may shape the emotional connotation of melodies[23]. Discrimination judgments are facilitated at accented locations in temporal patterns in the presence of regular, but not irregular, temporal contexts[24,25], even when the temporal information is irrelevant to the task[26]. Such observations support a view that attention is allocated dynamically to particularly salient moments in time[27]. Moreover, it is postulated that attentional processes are embodied in the brain as oscillatory processes—'attending rhythms'—that entrain to rhythmic properties in one's environment[27–29]. Multiple oscillators that are entrained to different hierarchical levels (periods) of pattern structure may be available for focusing attention during synchronization tapping[30]. Simpler joint melodic and rhythmic accent structures result in lesser variability during synchronization tapping than do more complex accent structures[31], further reinforcing a view that attention and timing are interwoven as part of a common mechanism involved in sensorimotor coupling to complex patterns.

In contrast to the short (<16 elements) sequences typically used in sequence learning experiments, real musical passages consist of hundreds or thousands of elements that can be readily memorized and recalled. Which of the behavioral aspects involved in learning short sequences can be generalized to the learning of musical sequences? According to recent studies, the early phase of sequence learning is often associated with predictions related to stimulus features, whereas continued training results in learning related to actual movements[32] or the consequences of movements[33]. As learning progresses, the subject is able to group or 'chunk' elements into larger combinations[34]. There is behavioral and computational support for this process of chunking[35]. For example, piano players first learn visual notation with individual sequential units linked together one at a time. With practice, they perceive and respond to the complete arpeggio as a single segment[36], and eventually this level of control can be maintained without resorting to responses based on shorter segments of information. Thus, individual elements become merged into higher-order programs[34,37].

Sequencing tasks have been used to examine chunking in experiments that manipulate the structural or relational aspects of individual elements, thereby influencing how they can be grouped into larger units. If a subset of sequential elements can be grouped according to a rule (for example, a spatial sequence of three adjacent fingers), RTs are shorter in response to elements within the sub-sequence than to the first element of the next sub-sequence[38,39]. Hierarchical organization of a longer sequence into a regular pattern of sub-sequences results in further chunking and reaction-time improvements[38]. Accentuating the temporal structure of a sequence by lengthening the response-to-stimulus interval at a fixed location in a repeating pattern also results in facilitated learning of the sequence[38,40]. Of particular interest is whether the joint-accent structure of musical sequences[27], an associated theory of dynamic attentional orienting[27,28], and concepts of hierarchical structuring in music[30,41] can predict how chunking processes unfold in learning a novel piece of music. For instance, at what point, if any, do salient temporal locations in musical phrases form chunking boundaries, and how are temporally salient locations on which expectations are focused related to the malleability of the internal timekeepers discussed above?

The neural circuitry of timing and sequence representations

Temporal and spatial sequence production in humans has been studied with functional neuroimaging for over a decade. Because sequences unfold in both time and space, their complexity varies

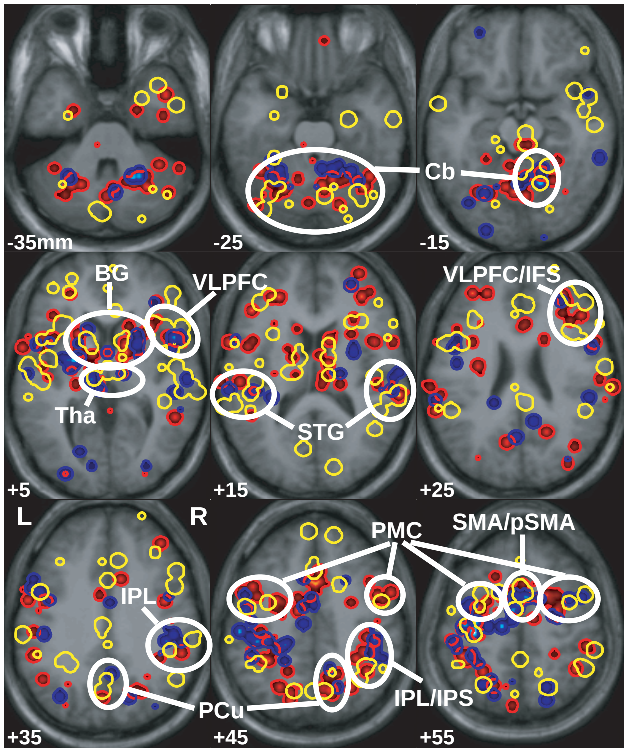

Figure 3 Projection of activation loci reported in 34 neuroimaging studies of sequencing (filled spheres) and 10 studies using musical stimuli and tasks (yellow outlines). Blue denotes activation foci from contrasts of simple sequencing behaviors with rest (13/33) or perceptual control conditions (20/33), whereas red spheres denote foci from 31 contrasts of complex movement conditions with less complex movement conditions, or contrasts that index explicit sequence learning or working memory. The music contrasts are more heterogeneous, involving various attentive, working memory, target detection and motor demands. See **Fig. 2** legend for anatomical abbreviations. See **Supplementary Note** online for additional information about this figure.

along both temporal and spatial (ordinal) dimensions (**Box 1**). Temporal complexity refers to the number of different durations that are perceived or produced during a task and to the presence of multiple durations that are metrically or non-metrically related. Ordinal complexity refers to the overall number of elements in a sequence, often represented by different spatial locations, that are to be learned or produced, and/or the number of effectors that are involved in producing a sequence. Individual studies are generally restricted in the number of points along these dimensions that they examine, and hold the complexity level of one dimension constant, usually implicitly, while manipulating complexity along the other dimension. The variance across experiments can be represented in a 'sequential complexity space' in which the component dimensions are temporal and ordinal complexity. The distribution of experimental conditions from 34 fMRI and PET studies within this complexity space is depicted in **Fig. 1**. The densities along the principal axes indicate that experimenters tend to manipulate complexity along one dimension while keeping the complexity of the other dimension relatively simple and constant, as in studies of learning and production of sequences of different length under isochronous pacing conditions.

Where does music fall in this complexity space? Music is generally of moderate temporal complexity (integer-ratio rhythms) and considerable ordinal complexity, due to long sequences of notes arising from multiple instruments or produced by multiple muscle groups. Typical music would exceed the scale of ordinal complexity in **Fig. 1**. However, because meaningful and satisfying musical experiences can consist of tapping simple rhythms to oneself or as part of a larger ensemble, or playing or singing a simple melody, music (or at least musical experience) might be considered to cover most of the complexity space in **Fig. 1**.

Using this complexity classification scheme for a meta-analysis of the neuroimaging literature on sequencing behaviors serves three purposes. First, it allows one to ask which brain areas are involved across complexity manipulations in both temporal and ordinal dimensions. Such areas might be considered to play an integrative role in sequencing behaviors. Second, it facilitates identification of areas that are modulated preferentially by one or the other dimension. In other words, if a brain area is primarily concerned with representing the spatial information about a sequence, the likelihood of its being activated should vary primarily with ordinal complexity. One should note that the term, 'complexity,' has an added dimension. Aside from a structural definition, used to describe the amount of spatial or durational variance in a sequence, complexity may also be defined in terms of the cognitive demands associated with processing a sequence. For instance, learning a structurally complex sequence may tax executive processes such as those involved with error monitoring or motor program structuring more than learning a simple sequence would. While structural complexity remains the same for any given sequence, cognitive complexity changes with learning. Music affords a wonderful system within which to study the acquisition of expertise in sequencing behaviors, though the issue of expertise is

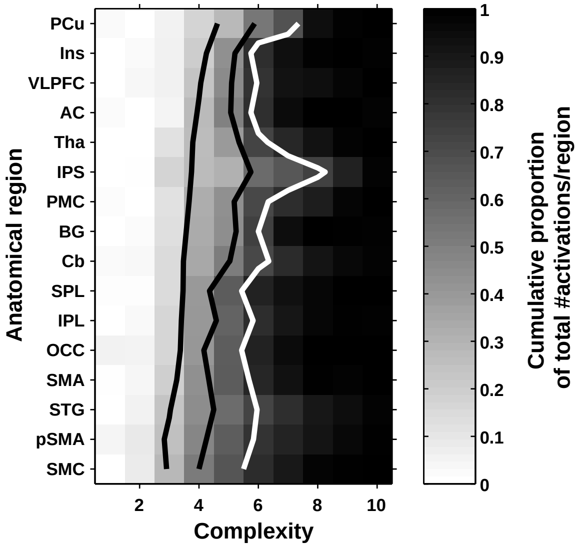

Figure 4 Cumulative proportions of the total number of reported activations for each brain region as a function of increasing complexity. Cumulative sums were obtained for each level of complexity by summing the number of reported number of activations in complexity grids of increasing size, beginning with the single square corresponding to temporal complexity = ordinal complexity = 1. The grids were enlarged at each complexity level by moving the top-right corner of the grid along the diagonal of the original complexity matrix. For each brain area, the cumulative sum was normalized by dividing the total number of observations for that area (see **Fig. 2**). The regions were rank-ordered by the sum of complexity columns 3 and 4. The contour lines show the 25, 50 and 75% intervals in the overall percentage of activations that are reported for a brain region. The slant in the 25% contour line indicates that some areas are more likely to become active as complexity increases.

beyond the scope of this review[42]. The final purpose of this meta-analysis is to provide a foundation for predicting how sequences of musical information might be organized by the brain by identifying regions of overlap in neuroimaging studies of sequencing and musical tasks.

Figure 2 shows how manipulations of temporal and ordinal complexity affect the recruitment of the 16 brain areas most commonly reported across the 34 neuroimaging studies. The sensorimotor cortex (SMC), supplementary motor area (SMA), cerebellum and premotor cortex (PMC) are sensitive to a broad range of temporal and ordinal complexity. A cluster analysis shows that the complexity patterns for cerebellum and PMC are relatively similar (**Fig. 2a,b**), and they show a greater proportion of activations at higher complexity levels, particularly temporal, than do the complexity patterns for SMA and SMC (**Figs. 2b** and **4**). The anterior cingulate, insula and precuneus are all primarily sensitive to manipulations of ordinal complexity under isochronous conditions. Although the basal ganglia, ventrolateral prefrontal cortex (VLPFC) and thalamus are also sensitive to manipulations of ordinal complexity under isochronous conditions, this latter group shows more sensitivity to increased complexity, both temporal and ordinal (**Figs. 2** and **4**), although not as uniformly as the cerebellum and PMC. The intraparietal sulcus (IPS) appears to be mostly sensitive to temporal complexity at low levels of ordinal complexity. Several authors have concluded that regions such as the cerebellum, SMA, PMC, basal ganglia and parietal cortex are involved in timing aspects of both perceptual and motor tasks[43–47] and might be considered important nodes in perception-action cycles. This set of areas is richly interconnected. Different parts of it may be biased toward either the timing or response selection aspects of the task[46–48]. Furthermore, within premotor cortex, different subdivisions may facilitate the perception of sequences associated with different motor-plan schemas[49].

Figure 3 provides a more detailed anatomical picture of the variability in the brain regions described above as a function of simple (blue) and more complex (red) sequencing behavior, as defined by the particular contrasts reported in the studies. Activations across different levels of complexity show considerable overlap in some regions such as the SMC and SMA/pSMA. While some areas of overlap are noted for the cerebellum, basal ganglia, thalamus, PMC, VLPFC, IPS and precuneus, all of which show greater proportions of activations at higher levels of complexity (**Fig. 4**), the partial segregation of blue and red clusters (**Fig. 3**) within these areas suggests that increases in complexity lead to differential and/or more extensive neural recruitment. Thus, our meta-analysis supports an overall view of a core circuit (SMC, SMA, cerebellum and PMC) that underlies sequenced behaviors, with tendencies toward regional differentiation and further recruitment of additional cortical and subcortical areas based on specific behavioral requirements.

Given that music inherently consists of sequential auditory and motor information, it might be expected that the perception and production of musical sequences will drive the same network described above. Indeed, several neuroimaging studies support a view of coupled perception and action (**Fig. 3**, white ellipses). The first neuroimaging study to examine the integration of perceptual (visual and auditory) and motor information in the context of sight-reading and playing music identified a circuit consisting of primary motor, medial and lateral premotor, superior parietal, lateral prefrontal and cerebellar areas[50]. While the superior parietal lobe and intraparietal sulcus appear to be generally involved in mapping symbolic stimuli to target locations for movements, restricted areas within these broader regions might be more specialized for translating a musical score[51]. In perceptual tasks, tracking the parts played by different voices/instruments in polyphonic music recruits medial and lateral premotor, parietal, cerebellar and basal ganglia structures, although the manner in which one listens (selectively or holistically, for example) influences the relative weighting of activation across these structures[52,53]. The task of listening to musical contexts and discriminating features of target events that complete or are embedded in the musical sequences recruits similar circuitry[53–57], although the specific detection or judgment of target events most commonly results in the activation of VLPFC[53–56,58]. Production of musical sequences has also been examined in the context of musical imagery tasks, in which subjects imagine a specific melody following a cue. Both perception and imagery of musical stimuli activate parietal, ventrolateral prefrontal and premotor areas[57,59,60].

Overall, there is considerable overlap of regions implicated in the perception-action cycle of music and areas involved in the perception, memorization and production of abstract sequences, although the number of non-overlapping music and sequencing/timing regions is striking (**Fig. 3**). This is due, in part, to the prominence of perceptual information in the conditions being contrasted in the music studies. The close apposition of many of the music-associated brain regions to sequenced-action foci (encircled areas in **Fig. 3**), and the consideration that some of the tapping and rhythm production tasks are somewhat musical in nature, increases the salience of these regions for further investigations of sensorimotor coupling in music. One question, which arises from the sequencing literature and pertains to the functional differentiation of lateral and medial premotor cortices, and which might be addressed in future music-sequencing studies, is whether playing a piece of music from a musical score (externally guided playing) tends to recruit lateral premotor areas more than playing a piece of music from memory (internally guided playing).

Implicit in the perception and production of sequences is the involvement of attention, even if the learning of a sequence is implicit, because the tasks demand that subjects respond to spatial cues, pacing tones or targets for which they are monitoring. Thus, neuroimaging studies of how attention is aimed in time are particularly relevant to this review's goal of linking theories and observations about attention, timing and sequencing into the context of music. The neuroimaging literature on attention is vast[61], yet few studies have directly addressed mechanisms underlying orienting of attention in time—an issue of central importance to music, given that sequences are sets of conjunctions of temporal intervals and other musical features. Brain activity increases in response to cues that predict when a visual event will occur in the immediate future throughout a bilateral network consisting of the VLPFC, SMA/pre-SMA, IPS, thalamus and regions of the temporal and occipital lobes[62]. When attention is aimed toward longer intervals (1,400 versus 600 ms), the thalamus, putamen and SMA show greater activation. When combined with orienting of spatial attention, orienting of temporal attention also recruits cerebellar and lateral premotor areas in addition to the areas listed above[63]. Together, these studies indicate that regions involved in orienting attention in time are largely the same as regions underlying sequencing behaviors. Activation of the basal ganglia as a function of the span over which attention is oriented is consistent with a role of the basal ganglia in maintaining representations of time intervals, partly in the service of attention[64], and the chunking of action representations[65–69].

Music and the orchestration of neural functions

Music offers the human mind a unique vehicle for thought, a means of experiencing various emotions, and an impetus to create sound and move in synchrony with one's environment. But what does it offer psychology and neuroscience? Music has motivated theories of attention in which temporal structure of sensory input induces attending rhythms that are conceptualized as oscillatory neural processes in a dynamical systems framework[27–29,70]. This type of framework can be used to model the characteristics of different types of neural timing mechanisms that underlie coordinated action and have been the focus of timing research for 30 years[5]. When collated across several domains of inquiry, the redundancy in the neuroimaging data calls for conceptual integration. Because music spans such a broad range of sensorimotor complexity, it provides a potential path for bridging the gap between abstract experimental tasks and real-world behavior.

Note: Supplementary information is available on the Nature Neuroscience website.

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