Synchronization and temporal processing
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Humans have the ability to flexibly synchronize motor output with sensory input, such as when dancing, performing, walking in step with a partner, or just tapping a foot along with music. The study of these behaviors, collectively called sensory-motor synchronization (SMS) offers an important window into human timing behavior and the neural mechanisms that support it. The study of SMS also provides insight into how the brain actively shapes our perception, general cognitive functions and our cultural social identity as humans. In this brief review, we will place SMS into a larger conceptual framework and highlight a rapidly expanding body of recent research.

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Basic SMS
Sensory-motor synchronization (SMS) refers to the coordinated temporal relationship between body movement and rhythmic patterns in the environment, typically in a periodic context [1,2]. As such, SMS implies not mere reaction to stimuli, but their anticipation, in order to enable phase locking with near synchrony as thoroughly reviewed by Repp and colleagues [3,4]. To summarize, SMS is canonically studied using paradigms in which participants tap a finger in time with a periodic stimulus such as a regular series of auditory beeps or visual flashes. The accuracy of synchronization is typically assessed with measures such as the mean and variance of tapping tempo and tap-to-stimulus asynchrony, or using circular measures such as phase-locking strength. SMS exists over a limited range of rates (~10 Hz to ~0.5 Hz), is often anticipatory, and is stable to perturbation. Two corrective processes have been proposed to maintain synchronization: phase correction (operating to minimize asynchrony between stimulus and response timing) and period
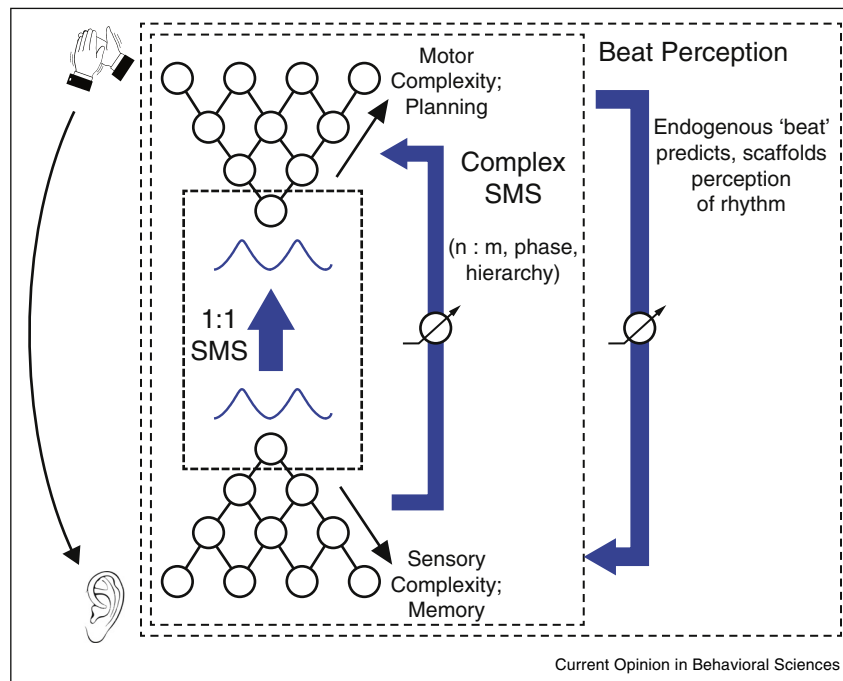
correction (operating to minimize tempo mismatch between stimulus and response). These features have traditionally been modeled from one of several perspectives: event-based (e.g. [5•]), or dynamical systems (e.g. [6•]).

SMS in context
Beyond the flexible capacity for overt synchronization of movement with stimuli, humans also possess a rich ability to internally model periodic timing that impacts perception even in the absence of movement. The precise mechanistic and phylogenetic boundaries between a simple capacity for SMS and a more internalized capability for complex beat, which we might call 'rich beat perception and synchronization' (rich BPS) are not agreed upon, and are blurred together in some accounts. Here we propose a conceptual model comprising three interacting, and potentially nested, neural architectures that seem necessary to account for the range of human timing behaviors (Figure 1): first, a neural link between sensory and motor systems, obviously needed for sensation to drive synchronized movement; second, hierarchical complexity of sensory and motor representations, needed to go beyond simple modes of synchronization to more flexible sensory-motor couplings; third, a reciprocal neural link from motor to sensory regions, needed for top-down control of perception by motor activity.

A first precondition for SMS is the presence of a neural link by which sensory activity can influence motor pattern generation (inner box). It is likely that these sensory-motor connections are not found in many animals [7]. Second (middle box), further elaboration of the complexity of temporal representations of sensation and motor planning, by feeding into basic synchronization mechanisms, could enable more complex and flexible patterns of synchronization. These include short-term pattern memory, subdivision, polyrhythms, metricality and flexibility in output effectors and patterns. Third (outer box), the presence of a reciprocal connection from the motor to sensory systems is proposed to open rich possibilities for an internal *sense of pulse* to influence how we organize and perceive rhythmic patterns, enabling rich BPS. The sense of pulse (or 'beat'), generated possibly by the motor planning system but yet divorced from both the need to move and from the external stimuli, may enable us to actively structure events in the flow of time (e.g. [8•]). In humans, at least, patterns of sound become *rhythms* only through interaction with our brains: Perception relative to a pulse gives sensory events rhythmic meaning, distinguishing for example up-beats from down-beats, and enabling perception of syncopation. In humans, these relationships can be further modified at will, implying

Figure 1

Conceptual hierarchy of neural architectures underlying human periodic timing abilities. The inner box encompasses 'basic' 1:1 SMS and requires a forward link between sensory (here, auditory) and motor processing (thick arrow). The middle box encompasses elaborations on sensory and motor representations that enable humans to flexibly select among more complex forms of synchronization. The outer box adds a link from motor to sensory systems to enable internal models of the beat to shape sensory processing. Willful control over transformations is indicated by nodes within the arrows.

the presence of additional mediating, transformative influences between sensory and motor systems.

Modality specificity

Entrainment to environmental stimuli is possible through many sensory systems: auditory, visual, tactile, or vestibular, but an auditory advantage has long been supposed. For SMS to temporally discrete auditory and visual stimuli (e.g. beeps versus flashes) an auditory advantage has been consistently found and ascribed to differential connectivity between auditory, visual and motor systems [9,10]. However, recent studies have shown that periodically *moving* 'bouncing' visual stimuli are able to drive discrete (tapping) synchronization with accuracy approaching or equal to auditory beeps [11–13]. These demonstrations suggest that synchronization performance depends more on the quality or modality-appropriateness of time representation than on modality per-se, with the compatibility of a stimulus with the sensory consequences of the synchronized movement in a given modality as a potentially important factor [14]. Supramodal mechanisms are supported by putamen activation that correlates with SMS accuracy, regardless of modality [12], and by similar evoked responses to visual and auditory stimuli in a tempo judgment task [15]. The ability of

non-auditory stimuli to drive more complex forms of rhythmic perception is only beginning to be studied, with several suggestions that moving visual stimuli may also be able to drive metrical perception [11,16,17]. Finally, it has recently been shown that auditory experience is not necessary for the development of robust synchronization: congenitally deaf individuals synchronize with visual inputs as well, or better than hearing individuals [11].

Entrainment and timing in movement production: event versus emergent timing

For many years, it had been assumed that sensorimotor timing is a general-purpose capability. This implies that someone with good sensorimotor timing skills at drawing would be a good piano player, implicating an effector-neutral clocking mechanism underlying the timing of all actions. Recent research has shown that this is not always the case. In particular, people who are highly skilled at finger tapping are not necessarily skilled at circle drawing and vice versa. The suggestion of multiple timing mechanisms has been confirmed by neuropsychological evidence showing that patients with cerebellar damage exhibited larger variability in finger tapping, but not for circle drawing [18]. It has been further suggested that two modes of timing exist: 'event' timing, under the

control of cerebellar processes, requires the existence of discrete events defining the timing task. By contrast, 'emergent' timing governs tasks for which timing emerges from the movement of the effectors, and is not thought to use cerebellar timekeeping resources [19•].

Recent studies [20] suggest that the invocation of event and emergent timing may not be solely due to cerebellar processes. When participants receive an auditory click or feel a tactile bump every time they cross a timing target during circle drawing [21], the pattern of errors for circle drawing resembles those seen in finger tapping [20]. It can be argued that the nature of event and emergent timing might have more to do with movement-specific sensory feedback than to kinematic or peripheral properties, arguing that the timing process also reflects perceptual goals. While continuous (emergent) and discrete (event-based) motor tasks might involve distinct timing mechanisms, they often co-exist in common human behaviors [22] and can be elicited by stimulus [23] or task demands [24,25]. Thus one could argue that both sensory and motor goals, or their combination, may lead to seemingly different timing strategies.

Neural substrates of SMS and BPS
The components of the brain involved in SMS, extensively studied using fMRI, have been reviewed recently [26,27••]. The latter is a meta-analysis of 43 studies demonstrating consistent activation of a range of cortical and subcortical structures: sensorimotor, premotor, supplementary motor and parietal cortex, along with basal ganglia and cerebellum. These regions were involved in different configurations for externally driven SMS versus internally paced continuation. Broadly, cerebellar circuits were active only during SMS, but not continuation, suggesting their importance for coordinating movement timing and stimulus-driven timing. Striatal areas were active for both SMS and self-paced tapping, suggesting a role in generation of periodicity. This interpretation complements the model of Teki *et al.* [28], which suggested cortical–cerebellar networks primarily compute sensorimotor asynchronies at a single interval level, while cortical–striatal networks exploit periodicity, perhaps through interval timing mechanisms proposed by the striatal beat frequency model [29]. It is tempting to map these systems onto behavioral observations of two error correction modes: phase and period [5•,30•], although there are alternative proposals [31]. Beyond basic SMS, more complex polyrhythmic synchronization results in activation of additional cortical areas including parietal and inferior frontal cortex (reviewed in [32]), while rhythmic manipulation may involve parietal cortex [33].

SMS can be modeled elegantly, for example, as depending on the behavior of systems of coupled oscillators [6•], as depicted conceptually in Figure 1. While this may be a

sufficient mechanistic model for simpler forms of SMS in some animals, neural mechanisms in humans are evidently more elaborate. It may well be that it was the evolution of overlap and interaction between the two timing mechanisms that enabled human SMS to emerge: indeed, the existence range of SMS closely corresponds to the temporal interval range over which both systems are active in interval timing [34].

While considerable progress has been made on describing the regions activated in beat perception, understanding of the dynamic activity and interactions of these regions during both SMS and beat perception is less fully explored. A number of studies have shown that sound-evoked brain responses are modulated by an internal beat [35–40], often in the beta band, which has suggested to numerous authors [38,39,41,42] that such modulation could have a motor origin. Complementing work in humans, Merchant and colleagues have examined SMS-related activity in macaques [43••].

Motor influences on perception
An important feature of human timing behavior is that internal models of periodic timing can influence the *perception* of rhythms (outer box in Figure 1). The notion that perception is active is an old one, from at least the time of Helmholtz, but one that is currently attracting a large amount of attention in neuroscience in general [44] and more specifically in the area of rhythm perception [31,32,45–47]. These accounts build either on the dynamic attending theory of Jones (e.g. [48]), on common-coding theories (e.g. [49–51]), or on motor theories of perception, which have a long history [52,53], and which we will focus on here. A core idea is that not only does sensory input drive motor planning, but that motor regions can also generate sensory predictions regarding the impact of planned or executed actions. A range of neural research supports a role of the motor system in generating perceptual predictions: cortical motor planning and striatal activity has consistently been observed while listening to, but not overtly synchronizing with, rhythms that induce a strong sense of periodic beat [54–57], motor areas show effectivity connectivity with sensory areas during beat perception [54], together with the beta-band involvement cited above.

The idea that motor structures are involved in perceptual judgments in general even when action is not required is gaining wide acceptance [58•,59••,60]. However, precisely *how* the motor system might impact auditory perception is not known, with proposals that it, acts suppressively [61], offers constraints for the existence range of beat perception [31], or serves as a source of sensory predictions that also shapes rhythmic perception, as in the ASAP (Action Simulation for Auditory Prediction) hypothesis [8•], which suggests that auditory processing uses the motor planning system as a source of

predictive inputs based on an abstract internal model of time, not necessarily tied to explicit motor simulation in ASAP, motor planning activity is not only used for prediction, but is also hypothesized to causally shape perception, through the dorsal auditory stream linking premotor, parietal and auditory cortices in order to implement bidirectional sound-motor transformations.

Evolutionary origins

The tendency to synchronize movement with sound, especially with others, appears to be universal in human culture and has been recognized by some as an important stage of human evolution, responsible in part for enabling the cohesion or advertising of larger social groups [62–64]. The origins of human rhythmic abilities are a matter of vigorous debate and speculation. Origin accounts of SMS range from being an adaptation for sexual selection, communication, group cohesion, to being a non-evolved side effect of other evolved traits (reviewed in [65]), and debate has been spurred by a recent spate of comparative studies exploring the limits of SMS in non-human animals including parrots, primates, and sea lions [66–71] as well as prior descriptions of naturally occurring SMS behaviors for instance in insects and frogs (reviewed in [72•]), and temporal sequencing and grouping abilities in other species [73]. There are many recent reviews of comparative SMS, some emphasizing the continuity of human abilities with those of other species, based on shared mechanisms (e.g. [72•,74]), with others seeking to explain why human abilities are not widely found in other animals, for example due to different patterns of brain connectivity (e.g. [8•,75]). In terms of the model of Figure 1, for the most part, only rudimentary (1:1) SMS represented by the inner box has been observed in other species and it is typically of limited flexibility in comparison with human SMS. To date, only a few species (vocal-learning birds and a sea lion) have been shown to be capable of 'Complex SMS' by synchronizing to the beat of more complex, musical stimuli, indicating a capacity to extract a beat from a complex auditory stimulus, and even to map flexibly to different motor outputs [66,69,76]. Evidence for hierarchical metrical perception or other aspects of rich BPS has not yet adequately been examined in non-human animals [77,78].

Future prospects

It is a time of plenty in rhythm research. We have reviewed a number of currently active fronts in the study of sensorimotor timing behaviors and their underlying neural mechanisms. Much work remains to be done in moving toward a complete description of the dynamic interactions between cortical and subcortical regions underlying SMS and beat-based perception, using a combination of human and primate electrophysiology, together with causal analysis and system perturbation using techniques such as transcranial magnetic stimulation to temporarily enhance or suppress local cortical function. Such

research will enable models and comparative theories to be increasingly grounded in specific brain circuits. A second hot topic is the degree to which training in SMS and complex beat perception might benefit non-musical abilities in the domains of language and cognition (e.g. [79••,80–83]). SMS research also raises important questions regarding sensory prediction mechanisms for action control when interacting with others. In particular, the question of how individual differences are manifest in these abilities needs to be addressed at the neural and behavioral levels [84,85]. Finally, comparative experiments attempting to test if animals possess more complex aspects of SMS and beat-based rhythmic behavior will be needed to further inform hypotheses of the origins of beat perception.

Conflicts of interest

Nothing declared.

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