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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

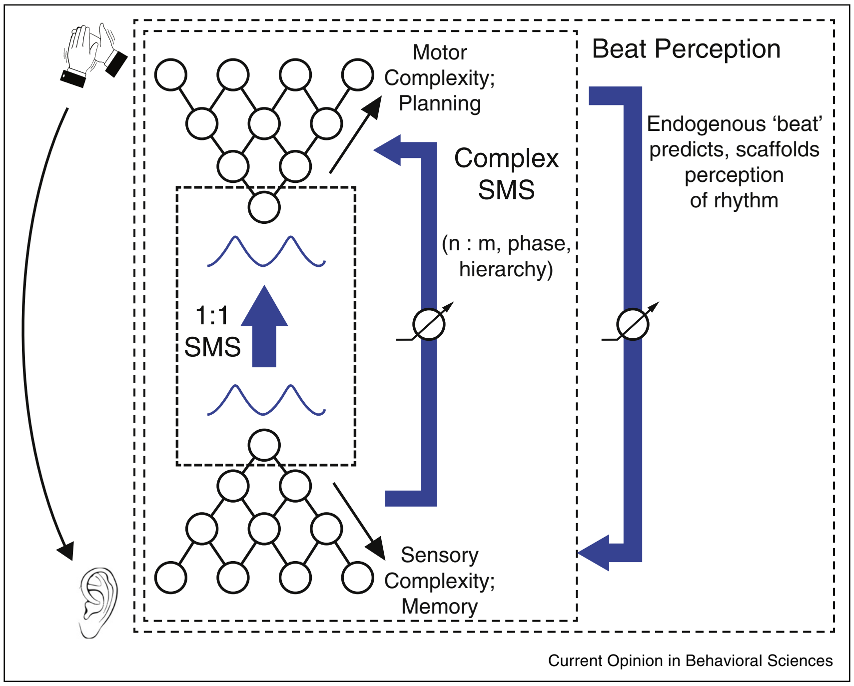
Sensory-motor synchronization (SMS) refers to the coordinated temporal relationship between body movement and rhythmic patterns in the environment, typically in a periodic context [1,2]. As such, SMS implies not mere reaction to stimuli, but their anticipation, in order to enable phase locking with near 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 ($\sim$10 Hz to $\sim$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