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Synchronization to auditory and visual rhythms in hearing and deaf individuals

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ABSTRACT

A striking asymmetry in human sensorimotor processing is that humans synchronize movements to rhythmic sound with far greater precision than to temporally equivalent visual stimuli (e.g., to an auditory vs. a flashing visual metronome). Traditionally, this finding is thought to reflect a fundamental difference in auditory vs. visual processing, i.e., superior temporal processing by the auditory system and/or privileged coupling between the auditory and motor systems. It is unclear whether this asymmetry is an inevitable consequence of brain organization or whether it can be modified (or even eliminated) by stimulus characteristics or by experience. With respect to stimulus characteristics, we found that a moving, colliding visual stimulus (a silent image of a bouncing ball with a distinct collision point on the floor) was able to drive synchronization nearly as accurately as sound in hearing participants. To study the role of experience, we compared synchronization to flashing metronomes in hearing and profoundly deaf individuals. Deaf individuals performed better than hearing individuals when synchronizing with visual flashes, suggesting that cross-modal plasticity enhances the ability to synchronize with temporally discrete visual stimuli. Furthermore, when deaf (but not hearing) individuals synchronized with the bouncing ball, their tapping patterns suggest that visual timing may access higher-order beat perception mechanisms for deaf individuals. These results indicate that the auditory advantage in rhythmic synchronization is more experience- and stimulus-dependent than has been previously reported.

1. Introduction

Rhythmic synchronization (the ability to entrain one's movements to a perceived periodic stimulus, such as a metronome) is a widespread human ability that has been studied for over a century in the cognitive sciences (Repp & Su, 2013). Across many studies, a basic finding which has been extensively replicated is that entrainment is more accurate to auditory than to visual rhythmic stimuli with identical timing characteristics (e.g., to a metronomic series of tones vs. flashes). Interestingly, when nonhuman primates (Rhesus monkeys) are trained to tap to a metronome, they do not show this modality asymmetry, and furthermore they tap a few hundred ms after each metronome event, unlike humans who anticipate the events and tap in coincidence with them (Zarco, Merchant, Prado, &

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Mendez, 2009). Thus, the modality asymmetry (and anticipatory behavior) seen in human synchronization studies is not a generic consequence of having a primate brain, and instead reveals something specific to human cognition.

In cognitive research, the auditory–visual asymmetry in human rhythmic synchronization accuracy is often taken as reflecting superior temporal processing within the auditory system. In the current study we asked if this asymmetry is indeed an inevitable consequence of human brain function, or if the asymmetry can be tempered (or even eliminated) by altering the characteristics of visual stimuli. In addition, we investigated if developmental experience plays a role in the accuracy of visual timing abilities and rhythmic perception by studying profoundly and congenitally deaf individuals.

1.1. Modality differences in temporal processing

The question of modality differences in the perception of time and rhythm has been a matter of debate for at least a century, and the question is of interest because it constrains theories of the cognitive architecture of timing. Is there an amodal timing center that can be accessed through the various senses, or is timing inherently tied to audition? Explanations have ranged from early claims that purely visual rhythm exists on an equal footing with auditory rhythm (e.g., Miner, 1903), to claims that any rhythmic sense one gets from a visual stimulus is due to an internal recoding into auditory imagery ('auralization', e.g., Guttman, Gilroy, & Blake, 2005). The former view is consistent with a more general timing facility, while the latter obviously ties timing uniquely to the auditory system.

Most existing research, and common experience, appear to support a significant deficit in rhythmic timing behavior driven by visual compared to auditory input. Evidence to date indicates that no discrete rhythmic visual stimulus can elicit the precise motor synchronization that humans exhibit to auditory rhythms (Repp & Penel, 2004). For the most part this view has been based on comparing synchronization with tones to synchronization with discretely timed visual stimuli (typically flashes), which are similar to tones in having abrupt onsets and a brief duration. When comparing tones and flashes, one observes significantly poorer synchronization with visual flashes (Repp, 2003), a dominance for sound in audio-visual synchronization paradigms (Repp & Penel, 2004), poorer recall of visual rhythmic patterns, despite training (Collier & Logan, 2000; Gault & Goodfellow, 1938), and temporal illusions in which the timing of an auditory stimulus influences perception of the timing of a visual stimulus (reviewed in Recanzone (2003)). The consistent superiority of audition in these studies has supported the idea that the auditory system is specialized for the processing of time, as expressed in the dichotomy "audition is for time; vision for space", a generally-accepted tenet that has guided much thought and experiment about the relationships between the modalities (Handel, 1988; Kubovy, 1988; Miner, 1903).

Poorer synchronization to flashing vs. auditory metronomes is surprising because the individual flashes generally occur at rates well within the temporal precision of the visual system (Holcombe, 2009). Although the flashes within visual rhythms are individually perceived, they do not give rise to the same sense of timing as do temporally equivalent auditory stimuli and thus cannot as effectively drive synchronization (Repp, 2003). This result has led to the suggestion that there is a fundamentally different mode of coupling between rhythmic information and the motor system, depending on whether the information is auditory or visual (Patel, Iversen, Chen, & Repp, 2005). This notion is supported by behavioral studies suggesting that flashes on their own do not give rise to a strong sense of beat (McAuley & Henry, 2010), and findings based on autocorrelation measures of successive inter-tap intervals suggest that the timing of taps to auditory and visual stimuli may be controlled differently (Chen, Repp, & Patel, 2002). Neuroimaging studies have also shown that synchronization with flashing visual stimuli depends on different brain regions than synchronization with temporally equivalent rhythmic auditory stimuli, including much stronger activation (during auditory–motor vs. visual–motor metronome synchronization) in the putamen, a region of the basal ganglia important in timing of discrete intervals (Grahn, Henry, & McAuley, 2011; Hove, Fairhurst, Kotz, & Keller, 2013; Jäncke, Loose, Lutz, Specht, & Shah, 2000; Merchant, Harrington, & Meck, 2013).

1.2. Temporal processing of moving visual stimuli

Although tapping to flashes lacks the precision of tapping to tones, there is ample evidence of precise visuomotor timing in other kinds of tasks. For example, the brain accomplishes precise visuomotor timing when moving objects and collisions are involved, e.g., when catching a ball or hitting a ball with a tennis racket (Bootsma & van Wieringen, 1990; Regan, 1992). Such visuomotor acts are typically not periodic, but it is possible that the accuracy demonstrated in such acts could occur when synchronizing with a moving visual stimulus with a periodic "collision point." A critical question, then, is how well synchronization can be driven by a moving visual stimulus with a periodic collision point. To address this question, we investigated visuomotor synchronization with a simulated bouncing ball that collided periodically (and silently) with the floor.

It is important to note that the synchronization behavior used in this study involves discrete movements (i.e., finger taps) aligned with discrete points in time (collision points), and is thus distinct from the large body of work demonstrating precise visuomotor timing in *continuous* movement synchronization with moving visual stimuli (e.g., Amazeen, Schmidt, & Turvey, 1995). While participants show a high degree of temporal precision in such continuous synchronization tasks, such synchronization is thought to employ a fundamentally different implicit timing mechanism than that involved in driving discrete, explicitly timed, rhythmic responses, which require explicit representation of temporal events (Huys, Studenka, Rheaume, Zelaznik, & Jirsa, 2008; Zelaznik, Spencer, & Ivry, 2002). Thus, we are asking how well discrete, repeated moments in time can be coordinated with moving visual stimuli.

There has been little research examining discrete rhythmic tapping to periodically moving visual stimuli. Recently, Hove, Spivey, and Krumhansl (2010) demonstrated that