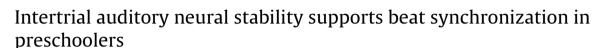
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ABSTRACT

The ability to synchronize motor movements along with an auditory beat places stringent demands on the temporal processing and sensorimotor integration capabilities of the nervous system. Links between millisecond-level precision of auditory processing and the consistency of sensorimotor beat synchronization implicate fine auditory neural timing as a mechanism for forming stable internal representations of, and behavioral reactions to, sound. Here, for the first time, we demonstrate a systematic relationship between consistency of beat synchronization and trial-by-trial stability of subcortical speech processing in preschoolers (ages 3 and 4 years old). We conclude that beat synchronization might provide a useful window into millisecond-level neural precision for encoding sound in early childhood, when speech processing is especially important for language acquisition and development.

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1. Introduction

Learning requires ongoing and repeated associations between stimuli and their implications (Hebb, 1949). Across modalities, stable perceptual representation of stimuli from one experience to the next allows for the emergence of coherent internal representations, while neural instability characterizes individuals with clinical disorders (e.g., autism, dyslexia, attention deficit, and schizophrenia; cf. Dinstein et al., 2015). This neural stability comes into play when an individual interacts with sound; unstable processing in the auditory system has been observed in individuals with language impairments (Ahissar et al., 2000; Evans et al., 2009; Hornickel et al., 2009; Hornickel and Kraus, 2013). Stable neural processing of structured temporal patterns may be particularly crucial for language acquisition and development: anticipation and detection of the timing of auditory events allows a listener

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to tune in to and predict important acoustic features (Large and Jones, 1999; McAuley et al., 2006) necessary for distinguishing and reproducing syllabic segments, prosodic cues, and the rapidly changing acoustic features that differentiate meaningful segments of speech (Baruch and Drake, 1997; Bertoncini and Mehler, 1981; Eimas et al., 1971; Ramus, 2000; Saffran et al., 1996; Tallal, 1980). Thus, stable neural coding of speech timing during early childhood - a period of intense, rapid learning and an age critical for mapping meaning to auditory input (Kuhl et al., 1992; Ruben, 1997) - could be acutely important for language learning.

Such precision and stability of speech processing in the human auditory system can be captured by examining the intertrial stability of the frequency following response (FFR) to a consonant-yowel speech syllable, a noninvasive measure of subcortical neural encoding, which records the summation of synchronous electrical activity originating from the auditory midbrain. The FFR reflects both temporal and spectral physiognomies of auditory stimuli with fine resolution (Skoe and Kraus, 2010). A high degree of intertrial stability of the FFR is associated with good reading ability in children, while intertrial variability has been observed to correlate with poorer reading skills (Hornickel and Kraus, 2013).

Beat synchronization, or entraining a motor movement to an auditory beat, has proved an intriguing tool for assessing sensorimotor timing (reviewed systematically in Repp, 2005; Repp and Su, 2013), and has been linked to the aforementioned intertrial

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neural stability of the FFR to speech in adolescents (Tierney and Kraus, 2013a,b). Synchronizing to an external beat likely relies on temporal fidelity for auditory perceptual coding, motor production, and coupling between auditory and motor systems (Sowiński and Dalla Bella, 2013). The auditory midbrain appears to be particularly important for beat synchronization, as it is uniquely positioned to play an integrating role: inferior colliculus receives ascending connections from subcortical auditory structures and motor areas (e.g., basal ganglia; Coleman and Clerici, 1987; Kudo and Niimi, 1980) and descending input from cortex (Bajo et al., 2010), in addition to sending information to cerebellum (another area crucial for fine motor control) via dorsolateral pontine nuclei (Hashikawa, 1983; Mower et al., 1979; Saint Marie, 1996).

Examining links between sound processing in auditory midbrain and beat synchronization could inform our knowledge of the biology responsible for transformation of perceived periodicity in auditory stimuli to motor output. Tierney and Kraus (2013a,b) have established a systematic relationship between intertrial stability of subcortical speech encoding and the consistency of beat synchronization in adolescents, proposing auditory system stability as a biological mechanism common to speech processing and beat-keeping. In young children, the ability to synchronize to a beat relates to precision of subcortical speech-envelope tracking, as well as pre-literacy skills thought to predict future reading skills such as phonological awareness and auditory short-term memory (Woodruff Carr et al., 2014).

Here, we expand upon previous work (Woodruff Carr et al., 2014) to explore the neurophysiology underlying individual differences in preschoolers who are able to synchronize motor movements to isochronous beats at prosodic stress rates. We predicted more consistent auditory-motor timing, as revealed through beat synchronization, would relate to higher levels of intertrial neural stability for processing speech syllables. Furthermore, our previous work identifying links between beat synchronization and neural envelope tracking precision led us to hypothesize that stability of low-frequency encoding in particular would relate to beat synchronization, because the envelope measure is filtered to capture low-frequency modulations. Our findings suggest that stability of auditory neural encoding may be an important foundation for sensorimotor integration in preschoolers. Furthermore, beat synchronization may serve as a useful behavioral tool for assessing developmental auditory neural function in young children.

2. Methods

2.1. Participants

Twenty-five children (15 females), ages three and four years old (M = 4.34, SD = 0.56), were recruited from the Chicago area. No child had a history of a neurologic condition, a diagnosis of autism spectrum disorder, a family history of language learning disorders, or second language exposure. All children had normal age-adjusted scaled scores for both verbal (M = 13.48, SD = 3.24) and nonverbal (M = 13.52, SD = 2.84) intelligence estimated with the Wechsler Preschool and Primary Scale of Intelligence, third edition (WPPSI; Pearson/PsychCorp, San Antonio, TX), passed a screening of peripheral auditory function (normal otoscopy, Type A tympanograms, and distortion product otoacoustic emissions at least 6 dB above the noise floor from 0.5 to 4 kHz) and had normal click-evoked auditory brainstem responses (identifiable wave V latency of <5.8 ms). Informed consent and assent was obtained from legal guardians and children, respectively, in accordance with procedures approved by the Northwestern University Institutional Review Board and children were monetarily compensated for their participation.

2.2. Beat synchronization

Our beat synchronization task was based on Kirshner and Tomasello's (2009) social drumming entrainment paradigm for preschoolers. The experimenter sat across from the child with two conga drums between them, one for the experimenter and one for the participant. Each conga had a Pulse Percussion DR-1 drum trigger attached to the underside of its drumhead to record the drum hits and convert vibrations into voltage in real time with no delay. The experimenter covertly listened and drummed to an isochronous beat presented through an in-ear headphone and encouraged the child to imitate and drum along with the experimenter. Auditory stimuli and drum hits of both the experimenter and participant were recorded as two separate two-channel recordings in Audacity version 2.0.5. Four trials were performed: two trials at 2.5 Hz followed by two trials at 1.67 Hz. Each trial was 20 s in duration, resulting in 50 isochronous drum hits for the 2.5 Hz trials and 33 drum hits for the 1.67 Hz trials. The use of two rates allowed for the assessment of general synchronization ability as opposed to synchronization to a specific rate, reducing the potential bias of an individual's preferred tempo.

2.2.1. Data processing

Synchronization data were processed using software developed in house in MATLAB (Mathworks, Inc., Natick, MA). Due to the high intersubject variability in intensity and rapidity of drumming, drum hits for the experimenter and participant were detected by setting an amplitude threshold and a refractory period on a participant-byparticipant basis. The first point at which the signal exceeded the amplitude threshold was marked as a hit, immediately followed by a refractory period during which the program did not mark peaks (to ensure multiple points were not marked for each hit). Accuracy of automated hit detection was checked manually to ensure onsets were correctly marked for each hit.

2.2.2. Data analysis

Beat synchronization ability was assessed using circular statistics (Fisher, 1993), a useful tool for assessing sensorimotor synchronization when there is not one-to-one correspondence of hits and pacing stimuli (Kirschner and Tomasello, 2009; Sowiński and Dalla Bella, 2013; Fujii and Schlaug, 2013), as is the case with this dataset: children frequently missed hits or did not synchronize continuously over a session. Each drum hit was assigned a relative phase angle (θ or "accuracy") in degrees by subtracting the hit time from the nearest experimenter's hit, dividing the result by the ISI, and multiplying by 360. The mean of all vectors resulted in R, a measurement of the extent to which participants tended to maintain a constant temporal relationship between their drum hits and the experimenter's. We define beat synchronization "consistency" as the average vector length across each of the two trials and across both rates. These two measures seem largely independent (correlation between consistency and accuracy: $r_{(25)} = -0.275$, p = 0.183). Recent work has shown the ability to synchronize to an external beat is still developing during this age (Kirschner and Tomasello, 2009; Woodruff Carr et al., 2014). Therefore, Rayleigh's test was applied to the set of all vectors produced in the two trials for a given rate to determine whether a participant was successfully synchronizing (the null hypothesis of this test is that the distribution of data points occur randomly in time near or away from the pacing stimuli onsets, indicative of chance performance; p > 0.05). The two trials at each rate were combined to compute a Rayleigh's pvalue for each rate. If a child's Rayleigh's test resulted in a p < 0.05at both rates, the child was included in analyses. Our previous work (Woodruff Carr et al., 2014) investigated group differences in neural processing between children who could (p < 0.05) and could not (p > 0.05) synchronize; the current investigation expands upon this

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