Title

Incorporation of feedback during beat synchronization is an index of neural maturation and reading skills

Authors

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Abstract

Speech communication involves integration and coordination of sensory perception and motor production, requiring precise temporal coupling. Beat synchronization, the coordination of movement with a pacing sound, can be used as an index of this sensorimotor timing. We assessed adolescents' synchronization and capability to correct asynchronies when given online feedback. Variability of synchronization while receiving Feedback predicted phonological memory and reading sub-skills, as well as maturation of cortical auditory processing; less variable synchronization during the presence of feedback related to more mature cortical processing of sound onsets and resting gamma activity. We suggest the ability to incorporate feedback during synchronization is an index of intentional multimodal timing-based integration in the maturing adolescent brain. Precision of temporal coding across modalities is important for speech processing and downstream literacy skills that rely on dynamic interactions with sound. Synchronization employing feedback may prove useful as a remedial strategy for individuals who struggle with timing-based language learning impairments.

1. Introduction
Speech comprises acoustic events such as syllables, word boundaries, and stress relationships that unfold over time to convey meaningful rhythms and patterns. These patterns are, however, not isochronous, as they fluctuate due to intentional (e.g. expressive contrasts) or artifactual (e.g. hesitations) motivations (Martin, 1972; Patel, 2010). Despite these timing variations, articulatory and syntactic constraints provide a predictable context for deciphering these patterns, allowing us to build a perceptual scaffold for directing attention to significant sound events while listening to dynamic speech (Jassem, Hill, & Witten, 1984; Lehiste, 1977). It has been suggested that this ability stems, in part, from endogenous, neurobiological oscillatory rhythms that entrain to the rhythmic structure of speech to generate temporal expectancies and facilitate allocation of attentional resources to periodic events (Bastiaansen & Hagoort, 2006; Fitzroy & Sanders, 2015; Giraud & Poeppel, 2012; Large & Jones, 1999; Large & Snyder, 2009; Nozaradan, Peretz, & Keller, 2016; Peelle & Davis, 2012).

When attending to sound, a listener must rely on precise encoding of temporal cues to inform perception, guiding actions, reactions, and adjustment of future action plans. This process requires intentional integration between neural systems involving auditory, visual, motor, parietal, and prefrontal circuits (Fetsch, Pouget, DeAngelis, & Angelaki, 2011; Nath & Beauchamp, 2011; Pasalar, Ro, & Beauchamp, 2010). From childhood to adulthood, experience-dependent learning occurs, sculpting the structural and functional architecture of these neural networks, and particularly the connections among them (Hebb, 1949). The incorporation of external experiences into mental representations allows for the construction of a neocortex capable of flexible reactions to novel exposures (Quartz & Sejnowski, 1997).

When it comes to speech communication, automatic and precise temporal coupling between auditory, visual, and motor areas in the brain is imperative for the integration of sensory perception and motor production. Work exploring auditory-motor synchronization has employed sensorimotor synchronization (SMS), or "beat synchronization", in which a participant is asked to entrain motor actions (e.g., tapping of a finger, striking a drum with a hand) to an isochronous auditory pacing stimulus (Bruno H. Repp, 2005; Bruno H. Repp & Su, 2013). This coordination of movement with sound has been used as an index of auditory-motor timing, and research suggests beat synchronization and speech processing rely on overlapping neural resources that facilitate temporal precision. Intriguing relationships have been observed between SMS variability and neural processing of speech (Tierney & Kraus, 2013; Woodruff Carr, Tierney, White-Schwoch, & Kraus, 2016; Woodruff Carr, White-Schwoch, Tierney, Strait, & Kraus, 2014), as well as language skills—particularly for reading (Tierney & Kraus, 2013; Woodruff Carr et al., 2014).

Unfortunately, some individuals' auditory systems struggle to keep up with these timing demands. A hypothesis has emerged implicating imprecise neural encoding of temporal cues, particularly at the prosodic rate of speech, in these individuals' auditory systems as a challenge contributing to speech and language processing disorders such as specific language impairment and dyslexia (Abrams, Nicol, Zecker, & Kraus, 2009; Goswami, 2011). It may also be the case that these individuals exhibit neurodevelopmental delays, compared to their peers.

Postnatal human cortical development unfolds over a much lengthier period than our mammalian relatives, with structural and functional plasticity extending into adulthood. The development of cortical regions is nonuniform, and longitudinal neuroimaging studies have discovered structural evidence that sensory cortices such as the auditory system exhibit changes in white and gray matter through adolescence (Giedd et al., 1999; Paus et al., 1999; Whitford et al., 2007), while maturation of higher-order heteromodal association cortices develop subsequently (Gogtay et al., 2004). These findings are complemented by electrophysiological functional observations that maturation of auditory-evoked potentials (Albrecht, Suchodoletz, & Uwer, 2000; Whitford et al., 2007). Cortical auditory evoked potentials (CAEPs) have been tracked through adolescent development, with reduction of P1 and increase of N1 amplitudes used as markers of auditory processing maturation (Bishop, Hardiman, Uwer, & von Suchodoletz, 2007; Fitzroy, Krizman, Tierney, Agouridou, & Kraus, 2015; Mahajan & McArthur, 2012; Ponton, Eggermont, Kwong, & Don, 2000).

Neural oscillatory activity also develops over the lifespan (Clarke, Barry, McCarthy, & Selikowitz, 2001; Whitford et al., 2007) and has been linked to brain maturation (John et al., 1980). Maturational changes have particularly been observed over adolescence ages in the gamma band, with resting-state activity decreasing into adulthood (Tierney, Strait, O'Connell, & Kraus, 2013). This developmental trend may have cognitive and linguistic consequences: as resting gamma increases with age in early childhood, infants with more gamma activity at rest develop better

language skills (Benasich, Gou, Choudhury, & Harris, 2008), while adolescents with less resting gamma perform better on reading-related tasks, following the developmental trend of decreasing gamma activity into adulthood (Tierney, Strait, & Kraus, 2014).

Insight into the development of timing-based multimodal integration during adolescence might be accomplished through an SMS task that requires online incorporation of performance feedback. Synchronization with feedback requires intentional, cognitive control of a typically automatic process. During synchronization tasks, humans tend to anticipate the beat (Aschersleben, 2002), but with the incorporation of feedback, participants would be forced to inhibit this natural tendency while correcting their timing to more accurately align with the beat onset. Given that prefrontal cortex and inhibitory processes are developing during adolescence, this could make synchronizing with feedback a useful metric for the maturation of attentional control and multi-modal integration mechanisms.

We suspect integration across auditory, visual, and motor modalities can reveal maturation of these systems, in particular the prefrontal circuitry involved in sensorimotor synchronization. To test this hypothesis, we had adolescents perform a beat synchronization task with and without visual feedback, and compared their ability to incorporate feedback to language skills, cortical processing of speech, and oscillatory activity. We predicted that those better able to incorporate feedback during beat synchronization would exhibit more mature neural processing of sound and advanced reading skills relative to their peers. This would provide both a lens into neurodevelopment and further evidence for the use of synchronization—with feedback—as a strategy for remediation.

2. Materials and methods
2.1. Participants.
Adolescents (N = 74, 38F, M = 17.96, SD = 0.98 years) were recruited from the Chicago area. All participants had normal pure tone hearing thresholds (<20 dB normal hearing level air conduction thresholds for octaves from 125 to 8000 Hz, with no apparent air-bone conduction gap), passed a screening of peripheral auditory function (normal otoscopy, distortion product otoacoustic emissions at least 6 dB above the noise floor from 750-8000 Hz) and click-evoked auditory brainstem response latency (identifiable wave V latency within lab-internal normal limits of 5.24-6.30 ms). No participant reported cognitive or neural deficits, nor did they report diagnosis of a reading disorder. Parental/guardian informed consent and adolescent informed assent (or participant consent if the participant was 18 years old) were obtained. The Institutional Review Board of Northwestern University approved all procedures, and participants were monetarily compensated for their participation.

2.2. Beat synchronization.
Beat synchronization was assessed using Interactive Metronome® (ClearTech Interactive), with the participant instructed to clap two hands together in a fluid circular motion against a hand trigger in time with a pacing tone delivered over headphones. Synchronization was performed at a rate of 0.9 Hz under two conditions: without feedback (No Feedback) for one minute, followed by synchronization with feedback (Feedback) for three minutes. During the Feedback condition, the participant saw a visual indicator on a computer screen of the asynchrony between their last clap and the 'target' beat (milliseconds before or behind the beat); see Figure 1 for schematic. These millisecond offset indications appeared in a colored box spatially corresponding to their offset in relation to the target, with each box representing a 30 ms window. If the participant clapped +/- 15 ms in relation to the target, the offset in milliseconds appeared in the green box. The example in Figure 1 represents a hit that was 27 ms early, so it appears in the yellow box to the left of the target. Interactive Metronome® provided hardware, software, and financial support for this project but were not involved in research design, analysis, or interpretation of results. The authors declare no personal conflicts of interest in Interactive Metronome®.

2.2.1. Data processing.
Synchronization asynchrony was assessed by calculating the average of asynchronies over each minute of the two feedback conditions. Synchronization variability during each condition was calculated as the standard deviation of asynchronies. Values were then log transformed to normalize variance.

2.2.2. Data analysis.
We compared only the last minute of the Feedback condition to the No Feedback condition to avoid the potentially confounding effect of learning to incorporate feedback on synchronization. Synchronization during the first minute of Feedback was different (larger asynchronies but less variable performance) than No Feedback (asynchrony: t_{73} = -2.995, p = 0.004, d = -0.357; variability: t_{73} = 2.517, p = 0.014, d = 0.322) suggesting a potential initial influence of

Feedback task learning on synchronization, combined with a practice effect from the prior No Feedback task. The last minute of Feedback did not differ from the No Feedback condition (asynchrony: t_{73} = -0.832, p = 0.408, d = -0.096; variability: t_{73} = 1.608, p = 0.112, d = 0.194), suggesting this comparison is more analogous across conditions. Synchronization between No Feedback and the last minute of Feedback were correlated (asynchrony: r_{68} = 0.290, p = 0.015; variability: r_{68} = 0.583, p < 0.001; controlling for participant age, sex, and verbal intelligence), indicating a relationship between performance on these tasks, but also demonstrating performance on these tasks is not identical across individuals.

2.3. Language and reading skills.
The following measures all produce age-normed standard scores. Performance on these language measures is inter-correlated to a moderate degree, as they may address overlapping skills or a general verbal intelligence quotient. Relationships between language and reading measures are reported in Table A.1.

2.3.1. Verbal intelligence.
To obtain a measure of vocabulary, the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999) vocabulary subtest was administered, in which the participant is asked to orally define written words. Verbal intelligence was not measured on one participant, and that participant was excluded from analyses controlling for this measure (N = 73, 37F, M = 17.97, SD = 0.98 years).

2.3.2. Working memory.
Working memory performance was assessed using the Woodcock-Johnson III Test of Cognitive Abilities (Woodcock, McGrew, Mather, & Schrank, 2001). Working memory is a cluster score from the Numbers Reversed and Memory for Words subtests. Numbers Reversed measures working memory by asking the participant to repeat a series of orally presented digits backward. Memory for Words is a verbal memory task that assesses echoic memory by requiring the participant to repeat a series of orally presented unrelated words. Working memory was not measured on four participants, and those participants were excluded from analyses using this measure (N = 70, 35F, M = 17.97, SD = 0.98 years).

2.3.3. Phonological Awareness and Phonological Memory.
Phonological Awareness and Phonological Memory were measured with the Comprehensive Test of Phonological Processing (CTOPP; (Wagner, Torgesen, & Rashotte, 1999). Phonological Awareness is a composite score of subtests Elision, in which participants create a new word by dropping a syllable or phoneme from a spoken word, and Blending Words, in which participants blend spoken syllables to create a new word. Phonological Memory is a composite score of Memory for Digits and Nonword Repetition subtests in which the participants repeat back a spoken list of increasingly longer digits or English-like nonwords. Phonological Awareness and Memory were not measured on five participants, and those participants were excluded from analyses using these measures (N = 69, 34F, M = 17.99, SD = 0.99 years).

2.3.4. Reading.
Reading is a cluster score measured by the Woodcock-Johnson III Test of Achievement (Woodcock et al., 2001). Reading is a cluster score from the Letter-Word Identification and Word Attack subtests, which are intended to assess sight vocabulary, phonics, and structural analysis. In Letter-Word Identification, participants read a list of words of increasing difficulty in isolation (rather than in context). In Word Attack, the participant pronounces nonsense words of increasing complexity. This cluster standard score is sex-normed. Reading was not measured on ten participants, and those participants were excluded from analyses using this measure (N = 64, 32F, M = 17.98, SD = 0.98 years).

2.3.5. Reading fluency.
Reading fluency was assessed using the Test of Word Reading Efficiency, Second Edition (TOWRE-2; (Torgesen, Wagner, & Rashotte, 2012). Reading fluency is a cluster score from the Sight Word Efficiency and Phonetic Decoding Efficiency subtests. In Sight Word Efficiency, the score is the number of printed words that can be accurately identified in 45 seconds. In Phonetic Decoding Efficiency, the score is the number of printed nonwords read in 45 seconds. Reading fluency was not measured on six participants, and those participants were excluded from analyses using this measure (N = 68, 34F, M = 17.99, SD = 0.99 years).

2.4. Cortical speech processing.

Cortical speech processing was assessed by the amplitude and latency of cortical auditory evoked potential (CAEP) components elicited by speech sounds. Cortical speech processing was not measured on nine participants, and those participants were excluded from analyses using these measures (N = 65, 33F, M = 18.00, SD = 0.67 years).

2.4.1. Stimuli.
CAEPs were elicited by a 170 ms six-formant stop consonant-vowel speech syllable [da] synthesized using a Klatt-based formant synthesizer (Klatt, 1980), presented 400 times at a 20 kHz sampling rate (for more information on the syllable, see Parbery-Clark, Skoe, & Kraus, 2009). The syllable consists of a voicing onset burst of broadband energy at 5 ms, a 50-ms formant transition, and a 120-ms steady-state vowel. The stimulus was presented via insert earphone (ER-3A) to the right ear in alternating polarities at 80 dB SPL at a rate of 0.99 Hz.

2.4.2. Recording parameters.
All recordings were made in an electromagnetically shielded soundproof booth. To decrease myogenic noise, participants sat in a reclining chair and watched a movie of their choice. The left ear remained unoccluded so that the participant could hear the movie's soundtrack (< 40 dB SPL). Cortical responses were collected at a sampling rate of 500 Hz with a bandpass of 0.05-100 Hz using a 31-channel tin-electrode cap (Compumedics, Charlotte, NC) referenced to linked earlobe channels. Electrodes were placed above the left pupil and outer canthus of the left eye to track vertical and horizontal eye movements. Individual electrode impedance was kept below 10 kΩ.

2.4.2. Data reduction and processing.
Cortical data were processed in MATLAB (The Mathworks, Inc., Natick, MA) using EEGLAB 12.0.1.0b (Delorme & Makeig, 2004) and ERPLAB 4.0.2.3 (Lopez-Calderon & Luck, 2014). Data were filtered offline from 1-35 Hz using a fourth order IIR Butterworth filter. Filtered responses were then epoched from -100 to 500 ms relative to stimulus onset. Epoched responses were baseline corrected to the average amplitude of the pre-stimulus period (100 ms). Epochs containing eyeblinks (VEOG voltage range exceeding 50 µV within a 150 ms moving window [120 ms increments]), eye movements (step-like HEOG voltage change exceeding 100 µV within a 200 ms moving window [50 ms increments]), or excessive noise (voltage exceeding ±170 µV at any electrode) were automatically detected and excluded from further analysis. Artifact-free responses were then averaged separately for each channel and participant.

2.4.3. Data analysis.
Latency of P1 was manually identified as the largest positive or polarity-inverting peak found between 40-100 ms. Latency of N1 was manually identified as the largest negative peak between 65-160 ms. These latencies were verified by two trained peak-pickers who simultaneously viewed average waveforms for every channel, as well as the across-channel average. Average waveforms across all 31 channels were then computed, and P1 and N1 amplitudes for each response were measured as the average amplitude in a 50-ms time window centered around the peak latency for that participant (responses with a P1 or N1 that was not prominent enough to be clearly picked were assigned the mean latency of all participants who had a clear P1/N1 to compute amplitude measurement). A composite measure of cortical onset response maturation was calculated as the difference in amplitude between N1 and P1; specifically, because N1 is a negative potential whereas P1 is a positive potential, P1 amplitude was subtracted from inverse N1 amplitude (Tierney, Krizman, & Kraus, 2015).

2.5. Intrinsic gamma activity.
Spectral power of intrinsic neural oscillatory power in the gamma frequency band (31-50 Hz) was recorded while participants rested. Resting oscillatory activity was not measured on twelve participants, and those participants were excluded from analyses using this measure (N = 62, 67F, M = 18.06, SD = 0.65 years).

2.5.1. Recording parameters.
Continuous electroencephalography (EEG) was recorded while participants sat in silence with eyes open for three minutes in a lighted soundproof booth. Participants were asked to rest while keeping their eyes open, fixate on a single point in the room (to minimize eye movement), and given no other task. Intrinsic gamma activity was recorded using the same equipment and parameters described for CAEP collection.

2.5.2. Data reduction and processing.
Continuous EEG activity was bandpass-filtered offline from 1-100 Hz (12 dB/octave rolloff). Eye-blinks, eye movements, excessive noise, or other artifacts were automatically detected and removed via spatial filtering in

NeuroScan Edit 4.3. The recording was segmented into 180 one-second non-overlapping epochs. The frequency spectrum of each epoch was calculated using a fast Fourier transform in MATLAB and the 180 frequency-spectra were averaged across all 31 channels. Gamma power was calculated as $20*\log10(x)$ where x is the mean amplitude from 31-50 Hz (range motivated by Tierney et al., 2013).

2.6. Statistical analysis.
Pearson correlations were performed between variables, and follow-up hierarchical multiple linear regressions were employed to partial out the influence of control measures (i.e., verbal intelligence, age, sex) and isolate the unique contribution of synchronization modification during Feedback (by controlling for synchronization variability during No Feedback) for measures that only correlated with Feedback variability. Statistics were computed using SPSS (IBM, Inc.).

2.7. Stimulus and Data Sharing.
All stimuli and data not under copyright restrictions are posted at http://osf.io/2ux3w.

3. Results
3.1. Feedback synchronization variability relates to reading-specific language skills.
To determine relationships between beat synchronization and language skills, correlations were calculated between synchronization asynchrony and variability during the two feedback conditions and measures of working memory, phonological awareness, phonological memory, reading, and reading fluency. Less variable synchronization (better performance) during Feedback correlated with better scores on all language tests, and particularly those assessing reading-specific skills (Table 1), while asynchrony during Feedback only related to working memory and phonological awareness.

No Feedback synchronization asynchrony did not relate to any cognitive or language test scores (all $p > 0.500$). No Feedback synchronization variability related to working memory ($r_{70} = -0.331$, $p = 0.005$) and phonological awareness ($r_{69} = -0.413$, $p < 0.001$), but did not correlate with phonological memory ($r_{69} = -0.202$, $p = 0.096$), reading ($r_{64} = -0.158$, $p = 0.213$), or reading fluency ($r_{68} = 0.083$, $p = 0.500$).

Synchronization asynchrony during Feedback only related to working memory (*WJIII*: $r_{70} = -0.323$, $p = 0.006$) and phonological awareness (*CTOPP*: $r_{69} = -0.299$, $p = 0.013$), while synchronization variability during Feedback was correlated with all measures of language skills administered: working memory (*WJIII*: $r_{70} = -0.334$, $p = 0.004$), phonological awareness (*CTOPP*: $r_{69} = -0.328$, $p = 0.006$), phonological memory (*CTOPP*: $r_{69} = -0.337$, $p = 0.005$), reading (*WJIII*: $r_{64} = -0.350$, $p = 0.005$), and reading fluency ($r_{68} = -0.296$, $p = 0.014$).

Follow-up hierarchical multiple linear regressions were performed to determine the unique predictive power of Feedback synchronization variability for the measures that only related to Feedback and not No Feedback synchronization. For each model, the first step included sex and verbal intelligence, while the second step controlled for No Feedback synchronization variability. In step three, Feedback synchronization variability was added to the model. (See Table 2 for ΔR^2's and Table A.1. for β's.)

3.1.1. Phonological memory.
The first step predicted unique variance in phonological memory ($R^2 = 0.115$, $F_{2,65} = 4.225$, $p = 0.019$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.032$, $F_{1,64} = 2.381$, $p = 0.128$). The addition of Feedback synchronization variability in the final step showed some evidence of improving model fit ($\Delta R^2 = 0.042$, $F_{1,63} = 3.280$, $p = 0.075$), resulting in a model that predicted 18.9% of variance in phonological memory ($F_{4,63} = 3.671$, $p = 0.009$).

3.1.2. Reading.
The first step (verbal intelligence only; WJIII accounts for sex differences in its scaled scoring) predicted unique variance in reading ($R^2 = 0.283$, $F_{1,62} = 24.470$, $p < 0.001$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.004$, $F_{1,61} = 0.342$, $p = 0.561$). However, the addition of Feedback synchronization variability in the final step did improve model fit ($\Delta R^2 = 0.067$, $F_{1,61} = 6.263$, $p = 0.015$), resulting in a model that predicted 35.4% of variance in reading skill ($F_{3,60} = 10.978$, $p < 0.001$).

3.1.3. Reading fluency.

The first step predicted unique variance in reading fluency ($R^2 = 0.124$, $F_{2,64} = 4.543$, $p = 0.014$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.029$, $F_{1,63} = 2.187$, $p = 0.144$). However, the addition of Feedback synchronization variability in the final step did improve model fit ($\Delta R^2 = 0.141$, $F_{1,62} = 12.419$, $p = 0.001$), resulting in a model that predicted 29.5% of variance in reading skill ($F_{4,62} = 6.484$, $p < 0.001$).

3.2. Cortical speech processing tracks with Feedback synchronization variability.

Synchronization asynchrony and variability during No Feedback were not related to amplitudes or latencies of cortical AEPs (*P1 amplitude*: asynchrony: $r_{65} = -0.107$, $p = 0.396$; variability: $r_{65} = 0.129$, $p = 0.306$; *P1 latency*: asynchrony: $r_{58} = 0.185$, $p = 0.165$; variability: $r_{58} = 0.103$, $p = 0.443$; *N1 amplitude*: asynchrony: $r_{65} = 0.008$, $p = 0.953$; variability: $r_{65} = 0.093$, $p = 0.461$; *N1 latency*: asynchrony: $r_{63} = 0.091$, $p = 0.483$; variability: $r_{63} = 0.101$, $p = 0.430$; *Cortical onset response maturation*: asynchrony: $r_{65} = 0.047$, $p = 0.712$; variability: $r_{65} = -0.122$, $p = 0.333$).

Synchronization asynchrony during Feedback also did not relate to any amplitudes or latencies of cortical AEPs (*P1 amplitude*: $r_{65} = 0.079$, $p = 0.533$; *P1 latency*: $r_{58} = 0.053$, $p = 0.693$; *N1 amplitude*: $r_{65} = 0.020$, $p = 0.875$; *N1 latency*: $r_{63} = 0.137$, $p = 0.286$; *Cortical onset response maturation*: $r_{65} = -0.051$, $p = 0.689$). On the other hand, synchronization variability during Feedback was moderately correlated with P1 amplitude and latency and N1 amplitude, with less variable synchronization during Feedback related to features associated with a more mature cortical response to sound onsets: a smaller, earlier P1 and a larger N1 (*P1 amplitude*: $r_{65} = 0.309$, $p = 0.012$; *P1 latency*: $r_{58} = 0.267$, $p = 0.043$; *N1 amplitude*: $r_{65} = 0.330$, $p = 0.007$; *N1 latency*: $r_{63} = 0.176$, $p = 0.167$; *Cortical onset response maturation*: $r_{65} = -0.361$, $p = 0.003$). See Table 1 for correlation values. Median splits of synchronization variability performance during Feedback were made to visually compare CAEP differences with regard to synchronization variability (Figure 2).

We performed hierarchical multiple linear regressions to compare the unique predictive power of synchronization variability during No Feedback and Feedback for CAEPs when controlling for demographic influences such as age, sex, and verbal intelligence. See Table 2 for ΔR^2's and Table A.2. for β's.

3.2.1. P1 amplitude.

The first step did not predict unique variance in P1 amplitude ($R^2 = 0.075$, $F_{3,60} = 1.623$, $p = 0.193$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.018$, $F_{1,59} = 1.161$, $p = 0.286$). However, the addition of Feedback synchronization variability in the final step did improve model fit ($\Delta R^2 = 0.101$, $F_{1,58} = 7.236$, $p = 0.009$), resulting in a model that predicted 19.4% of variance in P1 amplitude ($F_{5,58} = 2.783$, $p = 0.025$).

3.2.2. P1 latency.

The first step did not predict unique variance in P1 latency ($R^2 = 0.086$, $F_{3,53} = 1.662$, $p = 0.186$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.010$, $F_{1,52} = 0.575$, $p = 0.452$). The addition of Feedback synchronization variability in the final step ($\Delta R^2 = 0.062$, $F_{1,51} = 3.747$, $p = 0.058$) did not result in a significant model for predicting P1 latency ($F_{5,58} = 1.912$, $p = 0.109$).

3.2.3. N1 amplitude.

The first step provided evidence that the independent variables of age, sex, and verbal intelligence play a role in N1 amplitude ($R^2 = 0.149$, $F_{3,60} = 3.500$, $p = 0.021$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.003$, $F_{1,59} = 0.222$, $p = 0.639$). However, the addition of Feedback synchronization variability in the final step did improve model fit ($\Delta R^2 = 0.096$, $F_{1,58} = 7.384$, $p = 0.009$), resulting in a model that predicted 24.8% of variance in N1 amplitude ($F_{5,58} = 3.824$, $p = 0.005$).

3.2.4. Onset maturation index.

The first step provided evidence that the independent variables of age, sex, and verbal intelligence play a role in magnitude of the composite P1/N1 onset response ($R^2 = 0.133$, $F_{3,60} = 3.059$, $p = 0.035$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.010$, $F_{1,59} = 0.694$, $p = 0.408$). However, the addition of Feedback synchronization variability in the final step did improve model fit ($\Delta R^2 = 0.122$, $F_{1,58} = 9.584$, $p = 0.003$) to predict 26.4% of variance in onset amplitude ($F_{5,58} = 4.167$, $p = 0.003$).

3.3. Feedback synchronization variability tracks with maturation of intrinsic gamma activity.

To investigate differences in intrinsic oscillatory neural activity in the gamma band and its relationships to synchronization, we correlated synchronization asynchrony and variability during the two conditions and intrinsic gamma power (Table 1). Synchronization asynchrony in each feedback condition did not relate to gamma power (No Feedback: $r_{62} = 0.037$, $p = 0.777$; Feedback: $r_{62} = 0.223$, $p = 0.081$). No Feedback synchronization variability did not relate to intrinsic gamma power ($r_{62} = 0.198$, $p = 0.122$), but synchronization variability during Feedback did ($r_{62} = 0.408$, $p = 0.001$), with lower gamma power relating to less variable beat synchronization. As intrinsic gamma power decreases with maturation (Tierney et al., 2013), beat synchronization variability while incorporating feedback may index a maturational trajectory of neural oscillatory activity.

We performed a hierarchical multiple linear regression to compare the unique predictive power of synchronization variability during No Feedback and Feedback for gamma activity when controlling for demographic influences such as age, sex, and verbal intelligence scores that might affect oscillatory gamma activity in our sample (Tierney et al., 2013). See Table 2 for ΔR^2's and Table A.1. for β's.

The first step provides evidence that the independent variables of age, sex, and verbal intelligence play a role in intrinsic gamma activity ($R^2 = 0.212$, $F_{3,57} = 5.119$, $p = 0.003$). The addition of No Feedback synchronization variability in a second step did not improve the model ($\Delta R^2 = 0.025$, $F_{1,56} = 1.848$, $p = 0.179$). However, the addition of Feedback synchronization variability in the final step did improve model fit ($\Delta R^2 = 0.093$, $F_{1,55} = 7.623$, $p = 0.008$), resulting in a model that predicted 33% of variance in intrinsic gamma activity ($F_{5,55} = 5.424$, $p < 0.001$).

Follow-up comparisons were made between intrinsic oscillatory gamma power and the CAEP components to determine if there was redundancy between measures, and we determined that there were no correlations between gamma power and CAEP component amplitudes or latencies (*P1 amplitude*: $r_{61} = 0.150$, $p = 0.250$; *P1 latency*: $r_{54} = 0.168$, $p = 0.225$; *N1 amplitude*: $r_{61} = 0.147$, $p = 0.258$; *N1 latency*: $r_{59} = 0.057$, $p = 0.666$; *Cortical onset response maturation*: $r_{61} = -0.169$, $p = 0.194$). Furthermore, a hierarchical regression predicting Feedback synchronization variability from (step 1) demographics (step 2) CAEP onset maturation index and (step 3) intrinsic gamma power revealed CAEP and intrinsic gamma power contributed unique predictive power (*age, sex, verbal intelligence*: $R^2 = 0.062$, $F_{3,56} = 1.236$, $p = 0.305$; *cortical onset maturation index*: $\Delta R^2 = 0.098$, $F_{1,55} = 6.329$, $p = 0.014$; *intrinsic gamma power*: $\Delta R^2 = 0.137$, $F_{1,54} = 10.489$, $p = 0.002$). These cortical variables combined to predict 29.6% of variance in Feedback synchronization variability ($F_{5,54} = 4.550$, $p = 0.002$).

4. Discussion

This work reinforces evidence of a relationship between the ability to synchronize to a beat and cognitive and language skills (Corriveau & Goswami, 2009; David, Wade-Woolley, Kirby, & Smithrim, 2007; Flaugnacco et al., 2014; Thomson, Fryer, Maltby, & Goswami, 2006; Thomson & Goswami, 2008; Woodruff Carr et al., 2014) that extends into adolescence (Tierney & Kraus, 2013). For the first time to our knowledge, we extend this research to employ an online feedback task, revealing that synchronization variability, but not asynchrony, while correcting timing using explicit feedback also relates to working memory and phonological awareness, and uniquely relates to phonological memory, reading subskills, and reading fluency. Adolescents who synchronize less variably also score higher on these reading-related tests. Additionally, more mature auditory processing of speech onsets and intrinsic oscillatory gamma activity relate selectively to the synchronization variability during feedback task. These findings provide support for our initial hypothesis that timing-based modality-integration, as indexed by the variability of synchronization during the feedback task, improves with cortical maturation in adolescents.

The process of coordinating motor movements in time with an auditory pacing beat incorporates several elements: hearing the beat, tracking the beat to make predictions about the next occurrence, planning motor reactions to align movements to the beat, and adjusting these plans when a deviation between the auditory beat and timing of one's movement is detected. Incorporating visual information of these timing deviations (errors) must also be processed and integrated with error-correcting detectors in the auditory system. While auditory asynchronies exist in both experimental conditions, the Feedback condition's explicit representation of offset timing in the visual domain adds another layer of information to integrate and aid entrainment performance. While auditory feedback can be used to make very fine adjustments, responses to smaller perturbations of less than 20 ms are subliminal (Repp, 2001; Repp, 2000). The visual feedback provided in this task makes these small asynchronies explicit, which could contribute to differences between conditions.

Although we have previously demonstrated the importance of the auditory midbrain's temporal processing integration abilities for beat synchronization variability (Woodruff Carr, Tierney, White-Schwoch, & Kraus, 2016; Woodruff Carr et al., 2014; Tierney & Kraus, 2013), this is, to our knowledge, the first line of evidence that the ability to correct timing, assessed online, provides an index of cortical maturation.

Relationships between better (less variable) synchronization during feedback and reduction of CAEP P1 amplitude and an increase of N1 amplitude is consistent with previous work delineating maturational development across adolescence, both in cross-sectional (*P1:* Bishop et al., 2007; Cunningham, Nicol, Zecker, & Kraus, 2000; Mahajan & McArthur, 2012; McArthur & Bishop, 2002; Oades, Dmittmann-Balcar, & Zerbin, 1997; Ponton et al., 2000; Sharma, Kraus, J. McGee, & Nicol, 1997; Sussman, Steinschneider, Gumenyuk, Grushko, & Lawson, 2008); *N1:* (Bishop et al., 2007; Cunningham et al., 2000; Goodin, Squires, Henderson, & Starr, 1978; Mahajan & McArthur, 2012; L. Martin, Barajas, Fernandez, & Torres, 1988; McArthur & Bishop, 2002; Oades et al., 1997; Pang & Taylor, 2000; Ponton et al., 2000; Sussman et al., 2008) and longitudinal (Fitzroy et al., 2015) analyses. A reduction of P1 amplitude might reflect maturational synaptic pruning of the neural circuitry responsible for generating P1 and improved processing efficiency of P1-generating circuits. Synaptic pruning may also be responsible for an increase in N1 amplitude; decreases in gray matter density in parietal regions (Gogtay et al., 2004) that support attention (Buschman & Miller, 2007; Posner, Walker, Friedrich, & Rafal, 1984) may be indicative of pruning in inhibitory attentional circuits that would lead to disinhibition of neurons involved in generating the N1 CAEP.

Better synchronization variability during feedback also tracked with intrinsic oscillatory gamma power. High frequency (gamma) EEG oscillations are tied to cognitive processes such as attention (Fan et al., 2007; Fell, Fernández, Klaver, Elger, & Fries, 2003; Tiitinen et al., 1993), memory (Lisman & Idiart, 1995; Tallon-Baudry, Kreiter, & Bertrand, 1999), and the binding of sensory features into coherent percepts (Andreas K. Engel & Singer, 2001). These high frequency rhythms, both spontaneous and sensory-evoked, are generated in neural networks involving excitatory pyramidal cells and inhibitory gamma-aminobutyric acid (GABA) interneurons (Whittington, Traub, Kopell, Ermentrout, & Buhl, 2000). Gamma power decreases over the lifespan (Tierney et al., 2013; Whitford et al., 2007), and there is structural and functional evidence for two potential mechanisms at play that could result in decrease of gamma power with maturation. The first is that in adolescence (10-18 years of age), there is a loss of gray matter in frontal and parietal cortices (Giedd et al., 1999; Pfefferbaum et al., 1994; Steen, Ogg, Reddick, & Kingsley, 1997), which is interpreted as a reduction in synaptic density due to pruning. Individual resting EEG power has been linked to gray matter volume. Additionally, gamma activity may reflect the extent to which processing in distinct brain regions are coordinated (Engel, König, & Singer, 1991; Engel, König, Kreiter, & Singer, 1991). The areas that support language and reading are distributed throughout the brain; therefore an age-related decrease in gamma power, as observed from scalp electrodes, could also reflect greater localization, specialization, and efficiency of cortical processing with maturation (Benasich et al., 2008; Thompson et al., 2016; Tierney et al., 2014).

Due to the overlap in presumed underlying neural mechanisms (synaptic pruning), it might seem that changes in CAEP amplitudes and intrinsic oscillatory gamma power would be redundant measures: after all, a "better" brain at rest might also result in a "better" functioning brain. However, this does not seem to be the case; regression results reveal a lack of relationships between CAEPs and gamma power, and each contributes unique explanations of variance for synchronization variability during feedback. This is not necessarily surprising because P1 and N1 occur predominantly in the alpha region, and the low-pass filter for the CAEPs removes gamma band activity.

In light of the current findings, we suggest interventions based on beat synchronization might benefit individuals with timing-based language disorders, as this skill relates to reading abilities in adolescence and childhood (Tierney & Kraus, 2013; Woodruff Carr et al., 2014), and music training seems to improve both synchronization and reading skills (Slater, Tierney, & Kraus, 2013; Bhide, Power, & Goswami, 2013; Patel, 2011), possibly via motor structures (Chen, Penhune, & Zatorre, 2008; Kotz & Schwartze, 2010). Our findings also provide evidence that executive function networks involving the prefrontal cognitive control system are involved when incorporating performance feedback during timing remediation. Direct training of working memory and attention might also boost temporal processing, as evidenced by the success of training paradigms that explicitly train these cognitive skills (Anguera et al., 2013).

Training strategies aimed at improving underlying perceptual and motor processes have been under scrutiny in the learning disabilities community, and training studies have provided mixed evidence for generalization of

improvement beyond the training tasks to academic skills (Hammill, 1990; Vellutino, Steger, Moyer, Harding, & Niles, 1977). However, there is evidence supporting auditory training for the improvement of communication skills (Hornickel, Zecker, Bradlow, & Kraus, 2012; Merzenich et al., 1996; Tallal et al., 1996; Zuk et al., 2013), although negative results have also been reported (Hook, Macaruso, & Jones, 2001). The present findings provide a lens into adolescent neural maturation and consequent language skills, revealing relationships between a timing-based integration task and cortical auditory-evoked potentials, intrinsic oscillatory gamma activity, and reading subskills. These findings could be useful for clinicians seeking a monitoring tool for intervention outcomes, and future work is needed to determine if providing timing error feedback during synchronization could also be a successful strategy for remediation.

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Author Contributions

KWC and NK designed research; KWC, ABF, and AT performed research; ABF and AT contributed analytic techniques; KWC analyzed data; KWC, ABF, AT, TW-S, and NK wrote the paper.

Table Legends

Table 1.

	Cognitive, Language, and Reading Skills					Cortical Speech Processing					Intrinsic Oscillations
	Working Memory	Phonological Awareness	Phonological Memory	Reading	Reading Fluency	P1 Amp. (mV)	P1 Lat. (ms)	N1 Amp. (mV)	N1 Lat. (ms)	Onset response maturation	Gamma
No Feedback	-.331**	-.413***	-.202	-.158	.083	.129	.103	.093	.101	-.122	.198
Feedback	-.344**	-.328**	-.337**	-.350**	-.296*	.309*	.267*	.330**	.176	-.361**	.408**

Table 1. Correlations between cognitive, language, and reading assessments, cortical speech processing, intrinsic gamma activity, and synchronization variability during No Feedback and Feedback. Values reported are Pearson r-values. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Table 2.

	Reading Skills			Cortical Speech Processing				Intrinsic Oscillations
	Phonological Memory	Reading	Reading Fluency	P1 Amp. (mV)	P1 Lat. (ms)	N1 Amp. (mV)	Onset response maturation	Gamma
1. Demographics, Verbal Intel.	.115*	.283***	.124*	.032	.085	.093~	.070	.212**
2. No Feedback	.032	.004	.029	.017	.010	.003	.009	.025
3. Feedback	.042~	.067*	.141***	.091*	.058~	.086*	.110**	.089**
Total ΔR^2	.189**	.354***	.295***	.364~	.153~	.182*	.189*	.327***

Table 2. Regression models predicting reading skills, cortical speech processing, and intrinsic gamma activity from demographics (Step 1), synchronization variability during No Feedback (Step 2), and synchronization variability during Feedback (Step 3) conditions. Values reported are ΔR^2 for each step. ~ = $p < .08$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Figure Legends

Fig 1. During the Feedback condition, participants saw a visual indicator on a computer screen of the asynchrony between their previous clap and the previous target beat (milliseconds before or behind the beat). In this example, the participant clapped 27 ms earlier than the previous beat onset. Therefore, they can use this information to correct (in this case, lengthen) their interval judgment to more accurately align their clap to the next target beat.

Fig 2. Average cortical AEPs (to [da] syllable) for top- and bottom-half groups based on Feedback synchronization variability as a representation of the observed effect. Correlations are illustrated between Feedback synchronization variability and CAEP measures: P1 latency, P1 amplitude, N1 amplitude, and the derived cortical onset maturation index.

Appendices: Table Legends

Table A.1.

	Working Memory	Phonological Awareness	Phonological Memory	Reading	Reading Fluency
Working Memory		.583***	.661***	.432**	.468***
Phonological Awareness			.401**	.441***	.207
Phonological Memory				.459***	.401**

Reading					.562***

Table A.1. Inter-correlations between cognitive, language, and reading skill metrics. Values reported are Pearson r-values * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

Table A.2.

	Reading-related Language Skills			Cortical Speech Processing				Intrinsic Oscillations
	Phonological Memory	Reading	Reading Fluency	P1 Amp. (mV)	P1 Lat. (ms)	N1 Amp. (mV)	Onset response maturation	Gamma
Age	--	--	--	-.236~	-.070	-.262*	.279*	-.064
Sex	.039	--	.168	.009	-.085	-.200	.122	-.358**
Verbal Intel.	.285*	.488***	.240*	.143	.251	.135	-.155	-.151
No Feedback	-.023	.124	.463**	-.100~	-.085	-.172	.157	-.076
Feedback	-.263~	-.326*	-.487**	.406**	.322~	.396**	-.446**	.399**

Table A.2. Regression models from Table 2 predicting reading-related language skills, cortical speech processing, and intrinsic gamma activity from demographics and synchronization variability during No Feedback and Feedback conditions. Values reported are β-weights for each independent variable in Step 3 of Table 2 regression models. ~ = p < .08; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.