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# Musical Training Facilitates Exogenous Temporal Attention via Delta Phase Entrainment within a Sensorimotor Network

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Temporal orienting of attention plays an important role in our day-to-day lives and can use timing information from exogenous or endogenous sources. Yet, it is unclear what neural mechanisms give rise to temporal attention, and it is debated whether both exogenous and endogenous forms of temporal attention share a common neural source. Here, older adult nonmusicians ( $N = 47$ , 24 female) were randomized to undergo 8 weeks of either rhythm training, which places demands on exogenous temporal attention, or word search training as a control. The goal was to assess (1) the neural basis of exogenous temporal attention and (2) whether training-induced improvements in exogenous temporal attention can transfer to enhanced endogenous temporal attention abilities, thereby providing support for a common neural mechanism of temporal attention. Before and after training, exogenous temporal attention was assessed using a rhythmic synchronization paradigm, whereas endogenous temporal attention was evaluated via a temporally cued visual discrimination task. Results showed that rhythm training improved performance on the exogenous temporal attention task, which was associated with increased intertrial coherence within the  $\delta$  (1–4 Hz) band as assessed by EEG recordings. Source localization revealed increased  $\delta$ -band intertrial coherence arose from a sensorimotor network, including premotor cortex, anterior cingulate cortex, postcentral gyrus, and the inferior parietal lobule. Despite these improvements in exogenous temporal attention, such benefits were not transferred to endogenous attentional ability. These results support the notion that exogenous and endogenous temporal attention uses independent neural sources, with exogenous temporal attention relying on the precise timing of  $\delta$  band oscillations within a sensorimotor network.

**Key words:** Rhythm training; temporal attention; EEG; delta band; sensorimotor network; timing

## Significance Statement

Allocating attention to specific points in time is known as temporal attention, and may arise from external (exogenous) or internal (endogenous) sources. Despite its importance to our daily lives, it is unclear how the brain gives rise to temporal attention and whether exogenous- or endogenous-based sources for temporal attention rely on shared brain regions. Here, we demonstrate that musical rhythm training improves exogenous temporal attention, which was associated with more consistent timing of neural activity in sensory and motor processing brain regions. However, these benefits did not extend to endogenous temporal attention, indicating that temporal attention relies on different brain regions depending on the source of timing information.

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## Introduction

Attention is known to be deployable in both space and time. The allocation of attention, and hence the prioritization of the input of information, at a particular point in time is called temporal attention. Temporal attention plays an important role in our day-to-day lives as the precise and accurate prediction of timing results in optimized performance across numerous cognitive domains. For example, temporal attention is used to anticipate the onset of phonemes and words, which facilitate language comprehension (de Diego-Balaguer et al., 2016). It is also used to help time the gaps in traffic when attempting to cross a busy

street. Temporal attention can be further categorized into endogenous (top-down) and exogenous (bottom-up) mediated processes. Exogenous temporal orienting of attention takes place in response to rhythmic stimuli or stimuli with a predictable temporal structure, which is also referred to as beat-based or rhythmic timing (Coull and Nobre, 1998, 2008; Repp et al., 2008; Cravo et al., 2017). Thus, exogenous temporal attention refers to the process by which attention is oriented to the environment to drive internal timing representations. Endogenous temporal orienting of attention, on the other hand, relies on symbolic cues or nonrhythmic stimuli to infer timing information, and is also referred to as event-based, duration-based, or memory-based timing (Large and Jones, 1999; Olson and Chun, 2001; Nobre and van Ede, 2018). As such, endogenous temporal attention refers to the process by which attention is oriented internally for timing information. Interestingly, both exogenous and endogenous temporal attention becomes impaired with age, and negatively affects cognitive abilities that rely on the precise orienting of attention in time (Zanto et al., 2010, 2011, 2019; Bollinger et al., 2011; Padgaonkar et al., 2017). In this study, we aim to assess whether temporal attention in healthy older adults can be improved through musical rhythm (exogenous temporal attention) training, and to characterize the neuroplastic changes that underlie such improvements.

During musical performances, exogenous temporal attention is used to synchronize the musicians playing with rhythmic sources of timing information, such as a metronome, a conductor, or music from other band members. On the other hand, endogenous temporal attention is needed when rhythmic timing information is not available (as in a solo performance) and when a musician must rely on their own internal (memory-based) timing mechanisms. Thus, musical performances use both endogenous and exogenous temporal attention, albeit under different contexts. It is therefore not surprising that previous research has shown a musicianship advantage in both exogenous and endogenous timing abilities (Fränk et al., 1991; Rammsayer et al., 2012; Cameron and Grahn, 2014; Janzen et al., 2014; Zanto et al., 2019). Yet, it remains unclear whether exogenous and endogenous temporal attention relies on common neural mechanisms, which would enable training on one to improve the other. Here, we directly address this question by providing musical rhythm training for older adults with specific demands on exogenous temporal attention ability (i.e., synchronizing movements to beats). We then characterize the mechanisms that give rise to improvements in exogenous temporal attention and assess whether such changes transfer to improved endogenous temporal attention.

In support of the notion that exogenous and endogenous temporal attention utilizes a common neural network, a recent meta-analysis of exogenous and endogenous timing tasks have shown that both task types evoke activity in overlapping brain regions (Teghil et al., 2019). These regions include the supplementary motor area, intraparietal sulcus, inferior frontal gyrus, insula, and basal ganglia. Indeed, patients with basal ganglia degeneration have shown deficits in both exogenous and endogenous timing tasks (Cope et al., 2014), suggesting a critical role of the basal ganglia in timing ability. Furthermore, both exogenous and endogenous temporal attention has been associated with oscillatory neural activity within the  $\delta$  (1–4 Hz) (Stefanics et al., 2010; Gomez-Ramirez et al., 2011; Cravo et al., 2013; Arnal et al., 2015; Wilsch et al., 2015; Arnal and Kleinschmidt, 2017; Breska and Deouell, 2017),  $\alpha$  (8–12 Hz) (Praagstra et al., 2006; Rohenkohl and Nobre,

2011; Zanto et al., 2011; Breska and Deouell, 2014), and  $\beta$  (12–30 Hz) (Snyder and Large, 2005; Zanto et al., 2005, 2020; Androulidakis et al., 2007; Fujioka et al., 2009; Todorovic et al., 2015; Morillon and Baillet, 2017; Breska and Ivry, 2020; Graber and Fujioka, 2020) bands, although it remains unclear whether this oscillatory neural activity emanates from a common neural source. Nonetheless, these data collectively support models of a unified timing mechanism (Treisman, 1963; Miall, 1989; Ivry and Schlerf, 2008; Teki et al., 2012), which would enable musical training focused on exogenous temporal attention to yield benefits in endogenous temporal attention.

Conversely, there are numerous studies that suggest endogenous and exogenous temporal attention relies on separate neural mechanisms (Pashler, 2001; McAuley and Jones, 2003; Rohenkohl et al., 2011; Bouwer et al., 2020). There is a rich literature demonstrating that the cerebellum is uniquely involved in endogenous, not exogenous, timing tasks (Ivry et al., 2002; Spencer et al., 2005, 2007). Indeed, a double dissociation has been identified between patients with cerebellar or basal ganglia degeneration, such that the former exhibits a deficit in endogenous, not exogenous, timing, whereas the latter exhibits a deficit in exogenous, not endogenous, timing (Breska and Ivry, 2018). Endogenous temporal attention has also been uniquely associated with the inferior olive, whereas exogenous temporal attention has been uniquely associated with the putamen, caudate nucleus, and thalamus (Teki et al., 2011). This research supports models suggesting that timing is a distributed process that relies on modality- or context-specific neural regions (for review, see Mauk and Buonomano, 2004; Ivry and Schlerf, 2008; Paton and Buonomano, 2018). As such, if musical training that emphasizes exogenous temporal attention does not result in improvements in endogenous temporal attention performance, this supports the idea that these timing abilities rely on different neural mechanisms.

Understanding the source of temporal attention ability remains an active area of investigation. Although numerous brain regions and oscillatory signatures have been previously associated with temporal attention (as noted above), much less research has been dedicated to understanding which of these brain regions gives rise to this oscillatory activity. Here, we assessed changes in oscillatory EEG data during an exogenous temporal attention task both before and after rhythm training. Analysis focused on  $\delta$  phase coherence and  $\alpha$ /beta power in line with prior research that associated these frequency bands with temporal attention. Source localization was then conducted to elucidate which neural regions give rise to training-related changes in oscillatory signatures of exogenous temporal attention. Finally, we assessed whether rhythm training also improved endogenous temporal attention ability, which would address whether endogenous/exogenous temporal attention utilizes a common mechanism.

To achieve these goals, older adult (aged 60–79 years) nonmusicians were randomized to receive either rhythm training or active control training (word search). Older, rather than younger, adults were selected because we have previously demonstrated that older adults exhibit deficient performance on our assessments of exogenous (Zanto et al., 2019) and endogenous (Zanto et al., 2011) temporal attention. Selecting this population diminishes the likelihood that ceiling effects would mask potential training-related improvements. Pre-/post-training, exogenous temporal attention was assessed with a rhythmic synchronization paradigm that we have previously validated (Zanto et al., 2019).

This paradigm has been found to separate adults based on age and musicianship, such that young musicians exhibit the highest performance, followed by young nonmusicians, older musicians, and older nonmusicians in that order. We hypothesized that only the rhythm training group would exhibit improvements in exogenous temporal attention because only their training paradigm placed demands on exogenous temporal attention ability. To control for the possibility that sensory or motoric changes may have occurred following training, a sensorimotor response task was also implemented before and after training. Finally, to assess whether musical rhythm training benefits endogenous temporal attention, a temporally cued visual discrimination task was used before and after training. We have previously demonstrated that only younger, not older, adults benefit from predictive temporal cues during this task (Zanto et al., 2011). Here, we hypothesized that if exogenous and endogenous temporal attention share a common neural mechanism, then the rhythm training group would show an improvement in their ability to use predictive temporal cues and exhibit a similar change in oscillatory neural activity across the exogenous and endogenous temporal attention tasks.

## Materials and Methods

**Experimental design and statistical analysis.** In this preregistered study (Open Science Framework; <https://osf.io/fynpd>), participants were randomized to either a musical rhythm training group (Rhythmicity) or a word search training group (Control). Each group engaged with the training paradigm for 8 weeks (5 d per week, ~20 min per day) in their own home. Pre- and post-training, participants were assessed in-laboratory on their endogenous and exogenous temporal attention abilities, which served as the primary outcome measures for this study. Short-term memory performance was also collected, but not reported here as it is outside the scope of the temporal attention hypotheses and was published previously (Zanto et al., 2022). While engaged in the outcome assessments, EEG data were recorded.

Statistical analysis of behavioral performance used an ANOVA with a Greenhouse–Geisser correction when appropriate. To assess exogenous temporal attention, a rhythmic synchronization paradigm was used (described below) and analysis focused on performance asynchrony and variability. These data were submitted to separate ANOVAs with Group (Rhythmicity, Control) as a between-subjects factor and Time (Pre, Post) and Tempo (Slow, Medium, Fast) as within-subjects factors. Although circular statistics could be used to quantify performance asynchrony and variability, the calculation of circular statistics incorporates the tempo of the stimuli. As such, it is a biased measure when comparing across different tempos. Therefore, we opted to use linear statistics to quantify performance asynchrony and variability, which we have previously shown to be a more sensitive method to differentiate performance between age groups, tasks, and stimulus types (Zanto et al., 2019).

To assess endogenous temporal attention, a temporally cued visual discrimination task was conducted (described below). Analysis focused on accuracy and response time performance. These data were submitted to separate ANOVAs with Group (Rhythmicity, Control) as a between-subjects factor and Time (Pre, Post) and Condition (Predictive, Neutral) as within-subjects factors.

Finally, analysis of EEG data focused on event-related spectral perturbations (ERSPs) and intertrial coherence (ITC) in sensor space, as well as ITC in source space. *t* tests were used to compare between groups and time points (pre-/post-training). To correct for multiple comparisons, *p* values were cluster-corrected across electrodes/voxels based on Monte Carlo simulations. Corrected *p* values < 0.05 were considered significant.

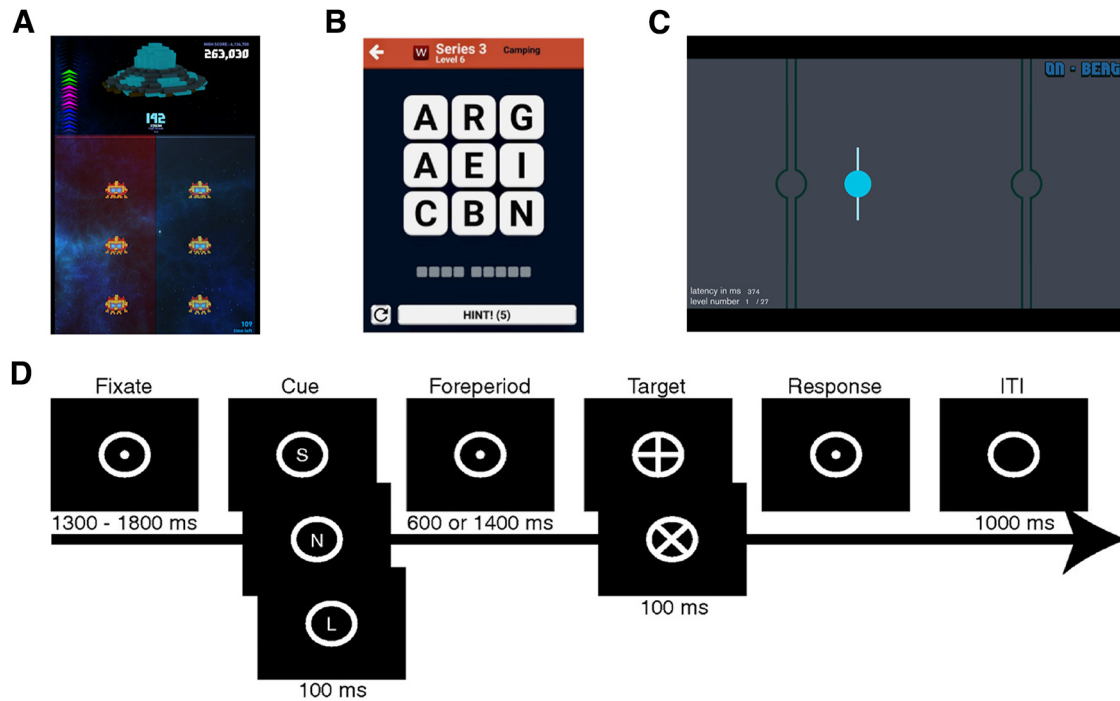
**Participants.** Forty-seven older adult nonmusicians aged between 60 and 79 years were recruited for this study (24 females). Nonmusicians were defined as having <3 years of formal instrument, song, or dance

instruction, and have not engaged in playing an instrument within the last year. All participants gave informed consent as approved by the University of California San Francisco Institutional Review Board. Participants were randomized into 1 of 2 groups: a musical rhythm training group (Rhythmicity) or a word search training group (Control). Both participants and researchers were blinded to the group assignments. Participants had no history of neurologic or psychiatric disease, no history of brain tumors, were not taking medications that modulate brain excitability (e.g., neuroleptic, antidepressant, stimulant, hypnotic), no amblyopia, strabismus, or color blindness, and had normal or corrected-to-normal vision and hearing. To ensure participants were cognitively healthy, all participants scored within 2 SDs of standardized scores on 12 tests of neuropsychological and physical function: California Verbal Learning Test-II, animal fluency, digit symbol, Patient Health Questionnaire, Delis-Kaplan Executive Functioning System Trails, Number and Number-Letter, Stroop, Measurement of Everyday Cognition, Ishihara Color Deficiency test, physical assessments (chair sitting and standing speed), hearing, and visual acuity. Five Rhythmicity participants were dropped from the study (3 for noncompliance, 2 for device malfunctions that prevented training/schedule adherence), resulting in 18 participants used for data analysis in the Rhythmicity group (mean = 67.7 years, SEM = 1.2, range = 60–79 years, 7 female). Five Control participants were dropped from the study (4 for noncompliance, 1 for technical problems during data collection), resulting in 19 participants used for data analysis in the Control group (mean = 69.0 years, SEM = 1.4, range = 62–78, 11 female). This number of participants in the final analysis was sufficient to achieve >80% power at a 95% significance threshold, based on our prior research with these temporal attention assessments in older adults (Zanto et al., 2011, 2019). Specifically, we calculated power using the smallest effect size from previously observed three-way interactions, which included 1 between-subject factor and 2 within-subject factors as implemented here. Participants received \$15 per hour for participation and a \$50 bonus for completion of the study.

**Training paradigms.** Musical rhythm training was conducted using a custom-designed video game, *Rhythmicity* (Fig. 1A). *Rhythmicity* was created at Neuroscape and incorporates closed-loop adaptive algorithms to consistently challenge cognitive function, which is thought to optimize training benefits (Mishra et al., 2016) and can be used to improve multiple cognitive abilities (Anguera et al., 2013; Mishra et al., 2014; Ziegler et al., 2019). It was played on a Microsoft Surface three tablet that permits tapping on a screen akin to certain types of drumming. Participants tapped the screen of the tablet in synchrony with the musical “beat,” which was also visually cued by moving targets (aliens). The game is designed to challenge rhythm and timing abilities, such that a nonmusician may learn to tap a steady rhythm. Adaptivity was built into *Rhythmicity* so that with practice, the rhythms become increasingly difficult, but if performance falters, the rhythmic demands become easier. As difficulty increases, participants subsequently accumulate more points. Difficulty of rhythms increased along three dimensions: tempo, complexity, and precision. Tempo refers to the speed of the rhythm, complexity refers to the number of taps required before the rhythm repeats (2, 4, or 8 taps), and precision refers to the amount of temporal offset allowed for a tap to be considered “on-beat.” During weeks 5–8 of training, the visual cues were presented so that participants may encode the rhythmic pattern into memory (as in weeks 1–4), but then the cues disappeared, and participants continued tapping the previously cued rhythmic pattern. In doing so, participants relied more on their working memory to produce the rhythmic pattern.

The Control group trained on a word search game, *Worder* (Fig. 1B), which was played on an iPad. *Worder* is a word search game that gets more difficult as the training progresses by expanding the field of letters to search. For example, *Worder* starts with a 3 × 3 grid of letters and advances to a 4 × 4 grid on sufficient progress. Hints were offered in case a participant gets stuck, but the number of daily hints was limited to maintain a challenging environment. Importantly, *Worder* places no demands on timing abilities, and so it was hypothesized that only *Rhythmicity* would result in enhanced temporal attention ability.





**Figure 1.** Training and Experimental paradigms. Screenshots from (A) Rhythmicity and (B) Worder (Control) training paradigms. Experimental design for (C) exogenous temporal attention task and (D) endogenous temporal attention task.

**Exogenous temporal attention assessment.** To assess exogenous temporal attention, participants were given a rhythmic synchronization paradigm (Fig. 1C), which was presented on a Microsoft Surface Pro 3 tablet, as previously described (Zanto et al., 2019). Briefly, this paradigm required participants to tap different metronome-like sequences on the screen of the tablet across 27 levels. These levels parametrically manipulated three variables: tempo of the metronome, the audiovisual information provided, and the rhythmic task performed. The tempo varied between slow (750 ms), medium (525 ms), and fast (350 ms) interonset intervals (IOIs). The stimuli presented varied between a visual-only stimulus where the movement of a ball between two lines on each side of the screen denoted the metronome “beat,” an audio-only stimulus where a distinct tone denoted the metronome “beat,” and an audiovisual stimulus where these cues were integrated. Last, participants were asked to perform three tasks: (1) on-beat: tap along with each stimulus event (i.e., beat: sound onset and/or when the ball touched the lines at either side of the screen); (2) off-beat: tap half-way between each stimulus event; or (3) continuation: after four stimulus events (i.e., 4 beats), the stimuli were discontinued, and participants had to continue the metronomic rhythm by tapping for 4 beats without disrupting the tempo. After the 4 beat “silent period” where participants were to tap, stimuli were resumed for another 4 beats and followed by another 4 beat “silent period” where participants were instructed to tap. The stimuli and silent periods continued to alternate for the duration of the level. Therefore, the “on-beat” task places the strongest demands on exogenous temporal attention as the stimuli references time points that index both the temporal duration to be encoded and used for subsequent temporal predictions, but also coincides with the time point where action is required. It is this convergence of action and perception based on extrinsic cues that enables exogenous temporal attention to play a central role in the on-beat task. Conversely, the “off-beat” and “continuation” tasks separate the action from the extrinsic timing cues. It could therefore be argued that this dissociation results in some reliance on endogenous temporal attention abilities, as memory for the encoded time interval cannot be updated at the time of action. Nonetheless, all three tasks (on-beat, off-beat, continuation) are useful to assess exogenous temporal attention abilities because, in each task, participants continually rely on extrinsic cues for timing information.

Together, the rhythmic synchronization paradigm consisted of 27 levels (3 tempos  $\times$  3 stimulus types  $\times$  3 tasks) each lasting  $\sim$ 30 s. To characterize exogenous temporal attention, performance asynchrony and variability were assessed. Asynchrony was calculated as the absolute offset in milliseconds from the instructed tap onset. Variability was calculated as the SD of tap offsets. Data were averaged over stimulus types and tasks to obtain an estimate of temporal attention ability.

**Sensorimotor response assessment.** A sensorimotor response assessment was conducted to determine whether changes in the rhythmic synchronization task were because of alterations in temporal attention or sensory/motor processing changes. Participants were instructed to respond as quickly as possible by pressing a button as soon as they perceived a stimulus. Participants were to fixate on a white fixation cross (60 point font) presented on a black background. Stimuli were presented for 100 ms randomly every 500–2500 ms. Stimuli were either an auditory 1000 Hz sine tone (auditory stimulus), a white circle (visual stimulus), or auditory-visual stimuli presented simultaneously. All visual stimuli were presented with a 200 pixel diameter at central fixation by temporarily replacing the fixation cross. Auditory stimuli were presented at a comfortable listening level using insert earphones (Cortech Solutions), which was held constant before and after intervention. Each stimulus type (auditory, visual, audiovisual) was presented in blocks of 50 trials. Each block of 50 trials was presented twice (once for each hand), resulting in 100 trials per stimulus type. Stimulus blocks were presented randomly across participants, but the order was held constant for each participant before and after intervention. Analysis focused on response times and response variability as measured by the SD of response times. Of note, one additional participant from the Control group was excluded from this specific analysis because of a technical error in data collection.

**Endogenous temporal attention assessment.** To assess endogenous temporal attention, a temporally cued visual discrimination task was conducted (Fig. 1D), as previously described (Zanto et al., 2011). A white circle with a 7 cm inner (8 cm outer) diameter was centered on a black background during the assessment. Participants were instructed to fixate on a dot (0.5 cm diameter) located in the center of the circle. The fixation period was between 1300 and 1800 ms (selected randomly). A 100 ms cue appeared and contained one of three letters: S, L, or N. These letters indicated the duration of the foreperiod (S = short = 600 ms; L = long = 1400 ms; N = neutral = 600 or 1400 ms). Thus, only S and L cues

**Table 1. Performance asynchrony and variability data from the exogenous temporal attention task<sup>a</sup>**

		Slow		Medium		Fast	
		Pre-training	Post-training	Pre-training	Post-training	Pre-training	Post-training
Asynchrony	Rhythmicity	151 (7)	143 (7)	118 (4)	114 (5)	94 (2)	92 (2)
	Control	152 (7)	148 (7)	120 (5)	117 (5)	99 (3)	100 (2)
Variability	Rhythmicity	132 (5)	116 (5)	107 (4)	96 (4)	80 (2)	81 (2)
	Control	135 (7)	138 (7)	106 (3)	104 (3)	81 (2)	81 (2)

<sup>a</sup>All data listed in ms. Numbers in parentheses indicate SEM.

predicted when the target would appear and will be referred to as PS (predictive short) and PL (predictive long), respectively. The neutral cues will be referred to as NS and NL, depending on whether the N preceded a short or long foreperiod, respectively. One of the four cue types (PS, PL, NS, NL) was selected randomly on each trial, each with a 25% probability. Following the foreperiod, a target appeared with either an x or a + inside the white circle, each with a 50% probability of occurrence. A forced-choice discrimination required participants to press the left button for x targets and the right button for + targets. Participants were instructed to respond with a button press as quickly and accurately as possible to the target. Thus, by using the temporally predictive cues, participants would be able to rely on their endogenous temporal attention abilities to facilitate performance. Specifically, engaging in the task enables participants to encode the cued time periods and form predictions for stimulus onset. It is this temporal encoding and prediction that enables attention to be allocated to target onset, resulting in speeded performance. Analysis focused on accuracy and response times to the PS and NS stimuli, in line with our previous observation of an age-related deficit in temporal attention ability (Zanto et al., 2011).

**EEG.** EEG data were recorded from a BioSemi ActiveTwo system with 64 Ag/AgCl active electrodes (Cortech Solutions). Signals were amplified and digitized at 2048 Hz with a 24-bit resolution and no online filter. All electrode offsets were maintained between  $\pm 20$  mV. EEG signal preprocessing and subsequent analyses were performed using EEGLAB (Delorme and Makeig, 2004) and MATLAB (The MathWorks). Raw EEG data were detrended to remove linear drift, bad electrodes were identified and corrected using spherical interpolation, and each channel was rereferenced against averaged EEG data. Independent component analysis was performed to remove eye blink and eye movement artifacts. Each EEG channel data was then down-sampled to 512 Hz and epoched into 2.2 s segments centered at stimulus onset. Epochs containing artifacts  $> \pm 75 \mu\text{V}$  were excluded from further analysis.

Spectral data (1–50 Hz) were acquired via complex Morlet wavelets applied to the epoched data. The log-transformed ERSP (Makeig, 1993) was then computed from the wavelet coefficients using a prestimulus baseline (–150 to –50 ms). For analysis of the exogenous timing task, a 300 ms time window was selected (75–375 ms after stimulus onset), which corresponded to peak ERSP activity when averaged over groups, conditions, and pre-/post-training sessions. ITC was computed from the phase angles obtained from the wavelet coefficients.  $\delta$  ITC was calculated using the following formula:

$$\frac{|\sum_1^N w e^{i\theta}|}{\sum w}$$

Where  $N$  = total number of trials,  $w$  = instantaneous amplitude, and  $\theta$  = instantaneous angle.  $w$  and  $\theta$  are derived from Morlet wavelet coefficients of time-series data. ITC values were obtained by averaging over each frequency band. Analysis of ITC data relied on the same time window as that used for ERSP analysis.

For source localization of ITC, the LORETA-KEY (Pascual-Marqui, 2002) software package was used. Epoched data were band pass filtered in the  $\delta$  band (1–4 Hz). Each of the filtered trials was then source localized using standardized low resolution electromagnetic tomography. The cartesian coordinate source localized current density output was then converted to spherical coordinates to obtain the azimuth and

elevation of the dipole within each voxel. The circular mean of the vector lengths from the azimuth and elevation angles were then calculated and averaged together to obtain the ITC of the source localized trials filtered in  $\delta$  frequency band.

## Results

### Exogenous temporal attention performance

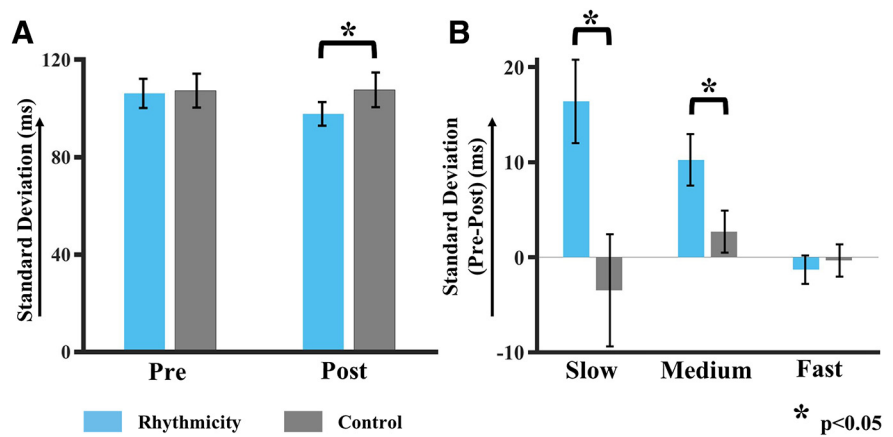
To assess exogenous temporal attention, performance asynchrony (offset in milliseconds from the instructed tap onset) and variability (SD of tap offsets) data (Table 1) were submitted to separate ANOVAs with Group (Rhythmicity, Control) as a between-subjects factor and Time (Pre, Post) and Tempo (Slow, Medium, Fast) as within-subjects factors. Results from the asynchrony data yielded a main effect of Tempo ( $F_{(2,70)} = 138.82$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.80$ ). Specifically, asynchrony was larger during slow compared with medium tempo ( $t_{(36)} = 10.12$ ,  $p < 0.001$ ), and the medium tempo exhibited larger asynchrony than the fast tempo ( $t_{(36)} = 9.61$ ,  $p < 0.001$ ). No other main effects were observed (Group:  $F_{(1,35)} = 0.52$ ,  $p = 0.47$ ,  $\eta_p^2 = 0.01$ ; Time:  $F_{(1,35)} = 2.09$ ,  $p = 0.16$ ,  $\eta_p^2 = 0.16$ ). Moreover, no interactions were observed between Group  $\times$  Time ( $F_{(1,35)} = 0.23$ ,  $p = 0.64$ ,  $\eta_p^2 = 0.01$ ), Group  $\times$  Tempo ( $F_{(2,70)} = 0.20$ ,  $p = 0.82$ ,  $\eta_p^2 = 0.01$ ), Time  $\times$  Tempo ( $F_{(2,70)} = 1.06$ ,  $p = 0.35$ ,  $\eta_p^2 = 0.03$ ), or Group  $\times$  Time  $\times$  Tempo ( $F_{(2,70)} = 0.04$ ,  $p = 0.96$ ,  $\eta_p^2 = 0.00$ ). Thus, training did not affect performance asynchrony.

Analysis of the performance variability data exhibited a main effect of Time ( $F_{(1,35)} = 7.02$ ,  $p = 0.012$ ,  $\eta_p^2 = 0.17$ ) such that performance variability decreased post-training. A main effect of Tempo was also observed ( $F_{(2,70)} = 151.13$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.81$ ), indicating that variability was larger during slow compared with medium tempo ( $t_{(36)} = 9.65$ ,  $p < 0.001$ ), and the medium tempo exhibited larger variability than the fast tempo ( $t_{(36)} = 10.91$ ,  $p < 0.001$ ). No main effect was observed for Group ( $F_{(1,35)} = 1.84$ ,  $p = 0.18$ ,  $\eta_p^2 = 0.05$ ). Importantly, significant interactions were observed for Group  $\times$  Time ( $F_{(1,35)} = 8.91$ ,  $p = 0.005$ ,  $\eta_p^2 = 0.20$ ) (Fig. 2A) and Group  $\times$  Time  $\times$  Tempo ( $F_{(2,70)} = 4.81$ ,  $p = 0.022$ ,  $\eta_p^2 = 0.12$ ) (Fig. 2B). Assessment of the Group  $\times$  Time interaction showed no differences in performance variability between groups at baseline ( $t_{(35)} = 0.24$ ,  $p = 0.81$ ), but the Rhythmicity group exhibited decreased performance variability post-training compared with the Control group ( $t_{(35)} = 2.32$ ,  $p = 0.026$ ; Fig. 2A). Assessment of the three-way interaction showed that performance improved (i.e., less variable) following rhythm training during the slow ( $t_{(17)} = 3.70$ ,  $p = 0.002$ ) and medium ( $t_{(17)} = 3.81$ ,  $p = 0.001$ ), but not fast ( $t_{(17)} = 0.86$ ,  $p = 0.40$ ), tempos (Fig. 2B). No such improvement was observed in the Control group pre- to post-training (slow:  $t_{(18)} = 0.60$ ,  $p = 0.56$ ; medium:  $t_{(18)} = 1.23$ ,  $p = 0.23$ ; fast:  $t_{(18)} = 0.19$ ,  $p = 0.85$ ). Direct comparisons between groups on the change (pre-post) in performance variability shows the Rhythm training group yielded an improvement in performance (i.e., less variable) during the slow ( $t_{(35)} = 2.69$ ,  $p = 0.011$ ) and medium ( $t_{(35)} = 2.19$ ,

$p=0.036$ ), but not fast ( $t_{(35)} = 0.68$ ,  $p=0.42$ ) tempos (Fig. 2B). No other interactions were observed (Group  $\times$  Tempo:  $F_{(2,70)} = 2.49$ ,  $p = 0.11$ ,  $\eta_p^2 = 0.07$ ; Time  $\times$  Tempo:  $F_{(2,70)} = 2.92$ ,  $p = 0.081$ ,  $\eta_p^2 = 0.08$ ). Together, these results show that musical rhythm training facilitated exogenous temporal attention as indexed by lowered performance variability.

Of note, the analyses above collapsed over three sensorimotor synchronization tasks to assess exogenous temporal attention in a manner that is less task-dependent. However, it could be argued that the continuation and off-beat synchronization tasks incorporate some aspects of endogenous temporal attention. Therefore, in an exploratory analysis, we repeated the above ANOVAs on performance variability for each of the three task types (averaged over stimulus type) to assess whether the two-way (Group  $\times$  Time) or three-way (Group  $\times$  Time  $\times$  Tempo) interactions would still be observed (Table 2). Results from the on-beat task replicated both the Group  $\times$  Time ( $F_{(1,35)} = 6.60$ ,  $p = 0.015$ ,  $\eta_p^2 = 0.16$ ) and Group  $\times$  Time  $\times$  Tempo ( $F_{(2,70)} = 3.49$ ,  $p = 0.043$ ,  $\eta_p^2 = 0.09$ ) interactions. Results from the continuation task exhibited a trend toward a significant Group  $\times$  Time interaction ( $F_{(1,35)} = 3.92$ ,  $p = 0.056$ ,  $\eta_p^2 = 0.10$ ), but not a Group  $\times$  Time  $\times$  Tempo interaction ( $F_{(2,70)} = 0.29$ ,  $p = 0.75$ ,  $\eta_p^2 = 0.01$ ). Results from the off-beat task exhibited no Group  $\times$  Time interaction ( $F_{(1,35)} = 1.56$ ,  $p = 0.22$ ,  $\eta_p^2 = 0.04$ ); however, the Group  $\times$  Time  $\times$  Tempo interaction trended toward significance ( $F_{(2,70)} = 2.94$ ,  $p = 0.081$ ,  $\eta_p^2 = 0.08$ ). Importantly, for all three tasks, even when interactions were not significant, the largest improvements pre- to post-training occurred in the Rhythmicity group at the slow and medium tempos. Nonetheless, this exploratory analysis indicates that improvements in exogenous temporal attention were driven by the task that had the largest exogenous (least endogenous) component.

For completeness, another exploratory analysis was conducted where we repeated the same ANOVAs as our original assessment of performance variability, but here we do it for each of the three stimulus types (averaged over task). We were specifically interested in whether the two-way (Group  $\times$  Visit) or three-way (Group  $\times$  Visit  $\times$  Tempo) interactions would still be observed as in the original analysis that averaged over all stimulus and task types. Results from the visual-only stimuli replicated both the Group  $\times$  Visit ( $F_{(1,35)} = 5.96$ ,  $p = 0.020$ ,  $\eta_p^2 = 0.15$ ) and Group  $\times$  Visit  $\times$  Time ( $F_{(2,70)} = 4.13$ ,  $p = 0.035$ ,  $\eta_p^2 = 0.11$ ) interactions. Results from the audio-only stimuli exhibited no significant interactions for either Group  $\times$  Time ( $F_{(1,35)} = 1.83$ ,  $p = 0.18$ ,  $\eta_p^2 = 0.05$ ) or Group  $\times$  Time  $\times$  Tempo ( $F_{(2,70)} = 0.87$ ,  $p = 0.42$ ,  $\eta_p^2 = 0.02$ ). Results from the audio-visual stimuli exhibited trends toward significance for both the Group  $\times$  Time ( $F_{(1,35)} = 1.56$ ,  $p = 0.22$ ,  $\eta_p^2 = 0.04$ ) and the Group  $\times$  Time  $\times$  Tempo interactions ( $F_{(2,70)} = 2.94$ ,  $p = 0.081$ ,  $\eta_p^2 = 0.08$ ). Importantly, for all three stimulus types, even when interactions were not significant, the largest improvements pre- to post-training occurred in the Rhythmicity group at the slow and medium tempos.



**Figure 2.** Response time variability performance during exogenous temporal attention task. Bar diagrams for interaction between (A) Group  $\times$  Visit (lower values indicate better performance) and (B) Group  $\times$  Visit  $\times$  Tempo (higher values indicate greater improvements).

### Sensorimotor response performance

Sensorimotor response performance was evaluated to test whether changes in performance from the temporal attention assessment may be attributed to sensorimotor changes. One additional participant from the control group was not included in this analysis because of errors in data collection. Response time and response time variability data (Table 3) were submitted to a mixed ANOVA with Group (Rhythmicity, Control) as a between-subjects factor, and Stimulus (Auditory, Visual, AudioVisual) and Time (Pre, Post) as within-subjects factors. Results from the analysis of response time data exhibited a main effect of Stimulus ( $F_{(2,68)} = 27.04$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.44$ ) such that response times were slower to Auditory stimuli compared with Visual ( $t_{(35)} = 5.35$ ,  $p < 0.001$ ) and AudioVisual stimuli ( $t_{(35)} = 5.67$ ,  $p < 0.001$ ). No significant difference in response times were observed between Visual and AudioVisual stimuli ( $t_{(35)} = 1.41$ ,  $p = 0.17$ ). No main effects were observed for Group ( $F_{(1,34)} = 0.00$ ,  $p = 0.99$ ,  $\eta_p^2 = 0.00$ ) or Time ( $F_{(1,34)} = 0.49$ ,  $p = 0.49$ ,  $\eta_p^2 = 0.01$ ). Additionally, no interactions were observed between Group  $\times$  Time ( $F_{(1,34)} = 0.94$ ,  $p = 0.34$ ,  $\eta_p^2 = 0.03$ ), Group  $\times$  Stimulus ( $F_{(2,68)} = 0.71$ ,  $p = 0.50$ ,  $\eta_p^2 = 0.02$ ), or Stimulus  $\times$  Time ( $F_{(2,68)} = 1.03$ ,  $p = 0.36$ ,  $\eta_p^2 = 0.03$ ). Similarly, no three-way interaction was observed between Group  $\times$  Time  $\times$  Stimulus ( $F_{(2,68)} = 1.41$ ,  $p = 0.25$ ,  $\eta_p^2 = 0.04$ ).

Results from the response variability data yielded no main effect of Group ( $F_{(1,34)} = 0.25$ ,  $p = 0.62$ ,  $\eta_p^2 = 0.01$ ), Time ( $F_{(1,34)} = 0.42$ ,  $p = 0.52$ ,  $\eta_p^2 = 0.01$ ), or Stimulus ( $F_{(2,68)} = 0.91$ ,  $p = 0.41$ ,  $\eta_p^2 = 0.03$ ). However, a significant interaction was observed between Group  $\times$  Time ( $F_{(1,34)} = 4.91$ ,  $p = 0.034$ ,  $\eta_p^2 = 0.13$ ). This interaction was driven by improvements in the Control (control) group pre- to post-training ( $t_{(17)} = 2.28$ ,  $p = 0.036$ ). No such improvement in performance was observed in the Rhythmicity group ( $t_{(17)} = 1.02$ ,  $p = 0.32$ ; see Table 3). No other interactions were significant: Group  $\times$  Stimulus ( $F_{(2,68)} = 0.51$ ,  $p = 0.60$ ,  $\eta_p^2 = 0.01$ ), Stimulus  $\times$  Time ( $F_{(2,68)} = 0.10$ ,  $p = 0.90$ ,  $\eta_p^2 = 0.00$ ), or Group  $\times$  Time  $\times$  Stimulus ( $F_{(2,68)} = 0.52$ ,  $p = 0.60$ ,  $\eta_p^2 = 0.02$ ). Together, results from the response time and response variability data indicate that rhythm training did not affect the sensorimotor response.

### Endogenous temporal attention performance

To test whether musical training also improved endogenous temporal attention, response time and accuracy data from the



**Table 2. Performance variability data from the exogenous temporal attention task<sup>a</sup>**

		Slow		Medium		Fast	
		Pre-training	Post-training	Pre-training	Post-training	Pre-training	Post-training
On-beat	Rhythmicity	85 (5)	65 (4)	75 (4)	65 (4)	72 (3)	70 (3)
	Control	86 (8)	85 (8)	76 (4)	73 (3)	74 (3)	75 (2)
Continuation	Rhythmicity	129 (6)	111 (7)	105 (5)	96 (5)	85 (3)	84 (2)
	Control	126 (8)	119 (8)	101 (4)	97 (6)	84 (3)	87 (2)
Off-beat	Rhythmicity	183 (11)	171 (10)	139 (7)	128 (7)	83 (4)	90 (4)
	Control	193 (15)	210 (13)	141 (6)	141 (7)	84 (4)	80 (4)

<sup>a</sup>All data listed in ms. Numbers in parentheses indicate SEM.

**Table 3. Data from the sensorimotor response assessment<sup>a</sup>**

		Audio		Visual		Audiovisual	
		Pre	Post	Pre	Post	Pre	Post
Response time	Rhythmicity	300 (7)	331 (27)	281 (6)	282 (6)	277 (9)	273 (6)
	Control	315 (11)	308 (7)	283 (8)	287 (7)	285 (8)	278 (6)
Response variability	Rhythmicity	58 (5)	70 (11)	62 (7)	63 (7)	61 (6)	69 (11)
	Control	82 (13)	67 (8)	58 (5)	58 (4)	73 (8)	60 (6)

<sup>a</sup>Response time and response variability (SD of response times) data listed in ms. Numbers in parentheses indicate SEM.

**Table 4. Response time and accuracy data from the endogenous temporal attention task<sup>a</sup>**

		Pre-training		Post-training	
		PS	NS	PS	NS
Response time	Rhythmicity	585 (20)	593 (21)	613 (27)	614 (21)
	Control	626 (32)	630 (31)	613 (21)	620 (20)
Accuracy	Rhythmicity	94% (2%)	94% (2%)	97% (1%)	97% (1%)
	Control	96% (1%)	96% (1%)	98% (1%)	98% (1%)

<sup>a</sup>Response time data listed in ms. Numbers in parentheses indicate SEM. PS, Predictive short cued trials; NS, neutral short cued trials.

temporally cued discrimination task were submitted to a mixed ANOVA with Group (Rhythmicity, Control) as a between-subjects factor, and Condition (PS, NS) and Time (Pre, Post) as within-subjects factors (Table 4). Results from the analysis of response time data exhibited no main effects for Group ( $F_{(1,35)} = 0.43, p = 0.52, \eta_p^2 = 0.01$ ), Time ( $F_{(1,35)} = 0.23, p = 0.64, \eta_p^2 = 0.01$ ), or Condition ( $F_{(1,35)} = 1.85, p = 0.18, \eta_p^2 = 0.05$ ). Additionally, no interactions were observed between Group  $\times$  Time ( $F_{(1,35)} = 2.09, p = 0.16, \eta_p^2 = 0.06$ ), Group  $\times$  Condition ( $F_{(1,35)} = 0.00, p = 0.96, \eta_p^2 = 0.00$ ), or Condition  $\times$  Time ( $F_{(1,35)} = 0.31, p = 0.58, \eta_p^2 = 0.01$ ). Critically, no three-way interaction was observed between Group  $\times$  Time  $\times$  Condition ( $F_{(1,35)} = 1.01, p = 0.32, \eta_p^2 = 0.03$ ).

Analysis of the accuracy data yielded a main effect of Time ( $F_{(1,35)} = 7.23, p = 0.011, \eta_p^2 = 0.17$ ), such that accuracy was greater post-training. No main effects were observed for Group ( $F_{(1,36)} = 2.03, p = 0.16, \eta_p^2 = 0.05$ ) or Condition ( $F_{(1,35)} = 0.54, p = 0.47, \eta_p^2 = 0.02$ ). Additionally, no interactions were observed between Group  $\times$  Time ( $F_{(1,35)} = 0.52, p = 0.48, \eta_p^2 = 0.01$ ), Group  $\times$  Condition ( $F_{(1,35)} = 0.89, p = 0.35, \eta_p^2 = 0.02$ ), or Condition  $\times$  Time ( $F_{(1,35)} = 0.01, p = 0.92, \eta_p^2 = 0.00$ ). Critically, no three-way interaction was observed between Group  $\times$  Time  $\times$  Condition ( $F_{(1,35)} = 0.11, p = 0.74, \eta_p^2 = 0.00$ ). Together, results from the response time and accuracy data provided no evidence that rhythm training transferred any benefit to endogenous temporal attention as indexed by the ability to use predictive temporal cues.

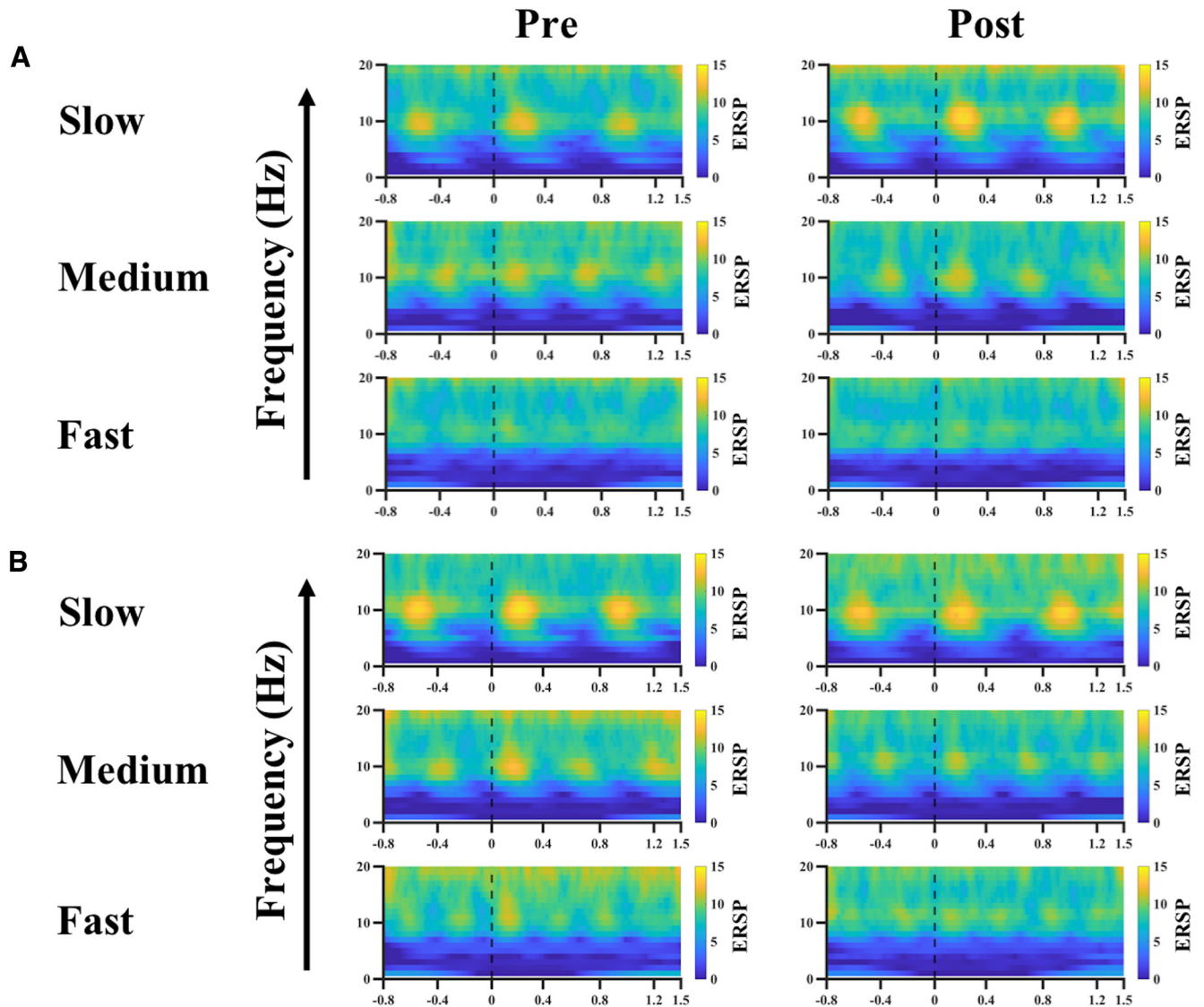
Although improvements in the ability to use the predictive temporal cues were not observed at the group level, we assessed

whether changes in exogenous temporal attention were related to changes in endogenous temporal attention, specifically within the Rhythmicity group. To do this, we first calculated an index of endogenous temporal attention as the difference in response times following the neutral and predictive cues (i.e., neutral minus predictive). Next, we conducted a Pearson’s correlation between the change (post-pre) in this index and the change (pre-post) in performance variability. Two correlations were conducted: one for each tempo where significant group effects were observed (i.e., slow and medium tempos). Results indicated no significant relationship between changes in exogenous and endogenous temporal attention abilities (slow tempo:  $r = 0.09, p = 0.74$ ; medium tempo:  $r = -0.05, p = 0.85$ ). These results converge with the analyses above to provide no evidence that exogenous temporal attention transferred any benefit to endogenous temporal attention ability.

**ERSP: exogenous temporal attention**

To understand whether oscillatory power changes may have occurred following rhythm training, ERSP was computed for the Rhythmicity and Control groups, pre- and post-training. The frequency bands of interest were  $\delta$ ,  $\alpha$ , and  $\beta$  because of their association with exogenous and endogenous temporal attention. Apart from these frequency bands, theta and  $\gamma$  bands were also assessed as a part of an exploratory analysis. ERSP was computed for each of these frequency bands, for each of the three tempos (slow, medium, and fast), averaged across all three conditions (on-beat, off-beat, and continuation). Visual inspection of the ERSP spectrogram shows  $\delta$  power desynchronization and  $\alpha$  synchronization peaks corresponding with the interstimulus interval for slow and medium tempos, but less so for the fast tempo (Fig. 3). Given the Group  $\times$  Time interaction observed in the performance variability data, statistical analysis of ERSP data focused on Group  $\times$  Time interactions (i.e., Rhythmicity Post-Pre  $\neq$  Control Post-Pre) that arose from differences within group (Post  $\neq$  Pre) and between groups (Rhythmicity  $\neq$  Control). Results showed a significant interaction for medium tempo in the alpha band. However, this was because of reduced  $\alpha$  ERSP post-training in the control group, and no significant





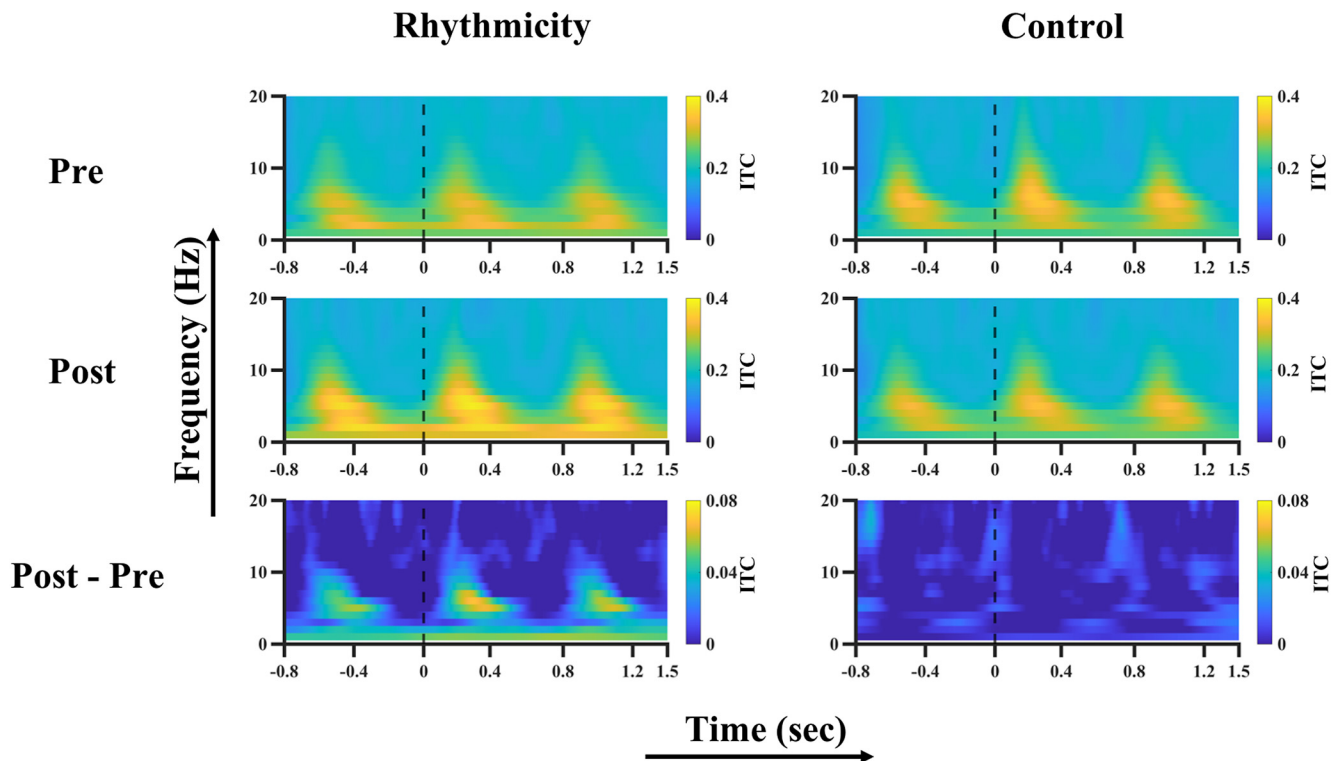
**Figure 3.** ERSP time-frequency map of electrode Cz for data from (A) the Rhythmicity group and (B) the Control group. The rows of each subplot are data from the different tempos. Columns represent pre-/post-training. Warmer colors represent increased ERSP. Vertical dashed line indicates stimulus onset.

difference was observed between groups pre- or post-training. Importantly, no other significant interactions were observed during the slow or medium tempos in any frequency band. Thus, ERSP data were not altered in a way that would explain training-related changes in performance.

#### ITC: exogenous temporal attention

Next, we assessed ITC for both Rhythmicity and Control groups, pre- and post-training, averaged across all conditions (on-beat, off-beat, and continuous) for each of the three tempos (slow, medium, and fast). Our main frequency band of interest was  $\delta$  because of evidences that phases of slow-frequency  $\delta$  oscillations are linked with temporal attention (Stefanics et al., 2010; Cravo et al., 2013; Wilsch et al., 2015; Arnal and Kleinschmidt, 2017; Breska and Deouell, 2017). However, we analyzed other frequency bands as exploratory measures: theta,  $\alpha$ ,  $\beta$ , and  $\gamma$ . Visual inspection of the ITC clearly showed increased coherence within the  $\delta$  and theta frequency bands following stimulus onset within both groups (Fig. 4), although the Rhythmicity group appears to show a greater increase in ITC after training (Fig. 4, bottom row).

To formally assess changes in ITC, we compared topographies between and within groups, in line the ERSP analysis, with a focus on Group  $\times$  Time interactions. Results showed a significant interaction (Post-Pre Rhythmicity vs Post-Pre Control) in  $\delta$  ITC for both slow and medium tempos (Fig. 5A, B, bottom right corner). These interactions were driven by changes within the Rhythmicity group pre- to post-training (see top row: Fig. 5A for slow tempo, Fig. 5B for medium tempo). Comparisons between groups showed no group differences before training, but greater ITC in the Rhythmicity group after training (Fig. 5A,B, middle columns). Because ITC is a measure of phase consistency across trials, these findings reveal that rhythm training results in more consistent neural activity patterns within the  $\delta$  band. Results from the other frequency bands showed no significant interactions in the  $\beta$  or  $\gamma$  bands. However, theta and  $\alpha$  bands exhibited an interaction during the slow, but not medium, tempo. Although these interactions were driven by changes in the Rhythmicity group pre- to post-training, no group differences were observed at either time point. Thus, changes in  $\delta$  band ITC are best aligned with the observed changes in performance.



**Figure 4.** ITC time-frequency map of electrode Cz during the slow tempo. Warmer colors represent increased ITC. Vertical dashed line indicates stimulus onset.

### Neuro-behavioral correlation

Since only the rhythm training group showed improved performance and increased ITC for the slow and medium tempos, we conducted a correlation between the change in performance and change in ITC to assess whether there was a relationship between these measures. Results from the slow tempo data showed a negative correlation between the change (post-pre) in ITC and the change (post-pre) in performance variability ( $r = -0.72$ ,  $p < 0.001$ ), such that, as ITC increases (i.e., becomes less variable), performance also becomes less variable (Fig. 6). No such correlation was observed during the medium tempo ( $r = 0.16$ ,  $p = 0.53$ ).

To understand whether the observed changes in  $\delta$  ITC during the slow tempo may be because of stimulus-evoked activity, we also analyzed ITC during the prestimulus period of  $-150$  to  $-50$  ms. Results mirrored that of the post-stimulus onset data reported above, such that a Group  $\times$  Time interaction was observed that was driven by changes in the Rhythmicity group pre- to post-training. Furthermore, this anticipatory  $\delta$  band ITC data showed a significant negative correlation with the change (post-pre) in performance variability ( $r = -0.71$ ,  $p = 0.001$ ).

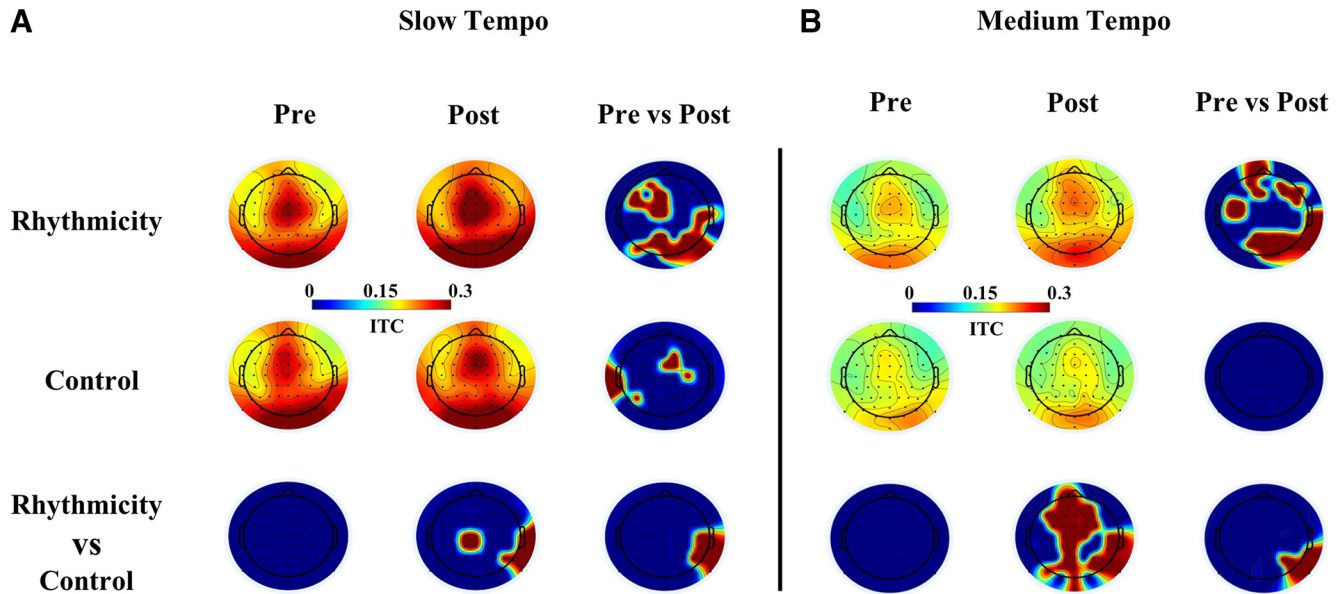
### Source localization

Given the significant neuro-behavioral correlation between ITC and behavioral data during the slow tempo, we sought to localize the source of phase synchrony to better understand which brain regions were responsible for the improvement in task performance. ITC was computed on  $\delta$  band filtered source localized EEG data from the post-stimulus time period. Following cluster correction using a Monte Carlo simulation ( $p = 0.0001$ ), ITC data were localized to three main regions: premotor cortex (MNI coordinate  $X = 7$ ,  $Y = -21$ ,  $Z = 53$ ), anterior cingulate cortex (MNI coordinate  $X = -5$ ,  $Y = 30$ ,  $Z = 28$ ), and inferior parietal

lobule extending into postcentral gyrus (MNI coordinate  $X = -63$ ,  $Y = 23$ ,  $Z = 29$ ) (Fig. 7).

### Discussion

In this study, our aim was to assess whether temporal attention in healthy older adults can be improved through musical rhythm training that specifically focused on exogenous temporal attention, and to understand the neural basis of such improvements, if any. We also assessed whether improvements in exogenous temporal attention would induce improvements in endogenous temporal attention. Behavioral findings indicated improved synchronization (less variance) to an external rhythm specifically in the rhythm training group, while no such change was observed in the control group. Given that no such changes were observed in a basic response time task, which controls for sensory and motoric processes, this result was interpreted as an improvement in exogenous temporal attention. We next analyzed electrophysiological data to understand the neuroplastic changes associated with improved exogenous temporal attention. Results showed an increase in ITC pre- to post-training in the  $\delta$  band, specifically in the musical rhythm training group. Importantly, the change in  $\delta$  ITC correlated with changes in performance in the rhythm training group, such that those participants who exhibited the greatest improvement in performance (more consistency) were the ones who exhibited the largest increase in  $\delta$  ITC (more consistency). Source localization of the  $\delta$  ITC data indicated neural generators within the anterior cingulate cortex, premotor cortex, inferior parietal lobule, and postcentral gyrus. Finally, assessment of performance from the endogenous temporal attention task exhibited no changes in either group post-training. Thus, there was no transfer of improvements to endogenous temporal attention after being trained on an exogenous temporal attention task. Together, these results indicate that musical rhythm training



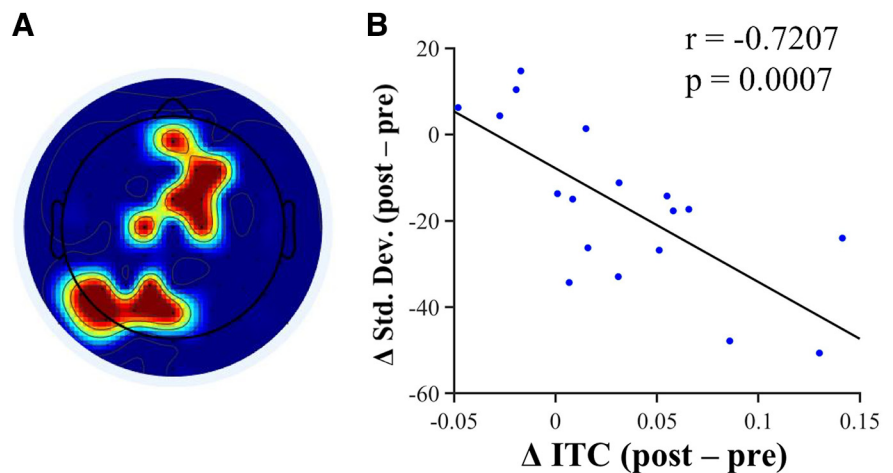
**Figure 5.** ITC topographies in the  $\delta$  band during the (A) slow tempo and (B) medium tempo. First row represents topographies from the Rhythmicity group pre-training (left), post-training (middle), and a pre- versus post-significance map (right;  $p < 0.05$ ). Second row represents topographies from the Control group, whereas third row represents significance maps when comparing between groups. Bottom right corner, Topography indicates a Group  $\times$  Time interaction. Top left corner, The four topographies are scaled according to the color bar. Bottom row and right column are significance maps where red represents significance ( $p < 0.05$ ) and blue represents not significant. All significance maps are cluster-corrected.

facilitates exogenous, not endogenous, temporal attention, which is associated with increased neural phase consistency (ITC) within a sensorimotor network.

To characterize training related changes in exogenous temporal attention, we used a synchronization task, which places demands on temporal attention as well as sensory and motor function. Therefore, it can be argued that the improvement in synchronization performance was because of changes in sensory or motoric processing. To test this possibility, we conducted a sensorimotor control task, which showed that performance did not change (Table 3). This indicates that the improvement in synchronization, as indexed by lowered variance (more consistency), was because of changes in temporal attention and not because of alterations in sensory or motor processing.

Interestingly, synchronization performance improved the most at the slowest tested tempo (750 ms IOI), with a smaller (albeit still significant) improvement at the medium tempo (525 ms IOI). Yet, performance at the fastest tempo (350 ms IOI) exhibited no improvements. We speculate that diminished signs of benefit from slow to fast tempos may be attributed to preferred tempos. The slowest tempo tested was closest to the preferred tempo for adults in this age range, whereas the medium and fast tempos are preferred among young adults and children, respectively (Mcauley et al., 2006). Although we did not test for preferred tempos, these results lead to an interesting possibility that tempo preferences may be related to exogenous temporal attention.

Previous research has shown that exogenous timing abilities can improve with training. This has been seen in studies comparing musicians and nonmusicians, where years of musical training

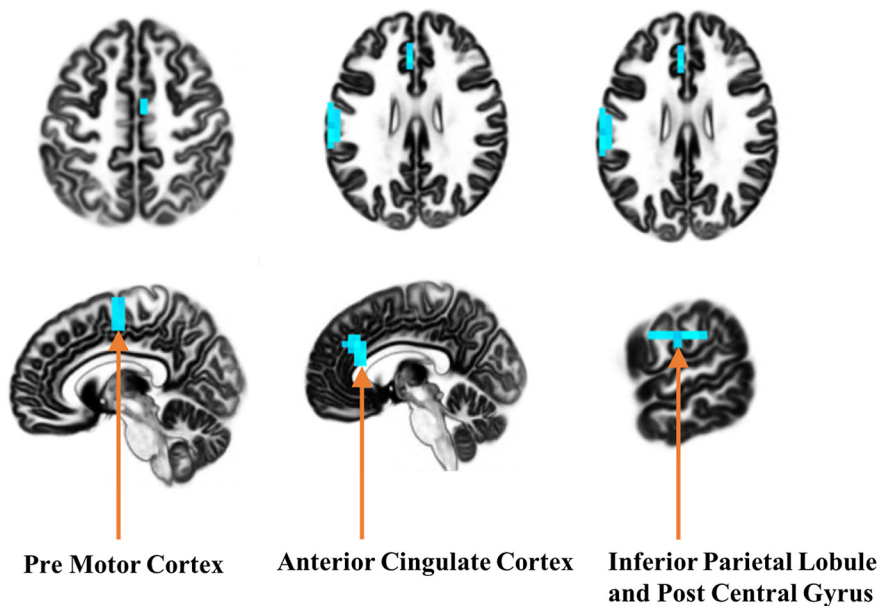


**Figure 6.** Neuro-behavioral correlation. A, Cluster-corrected topography showing significantly correlated regions (shaded in red;  $p < 0.05$ ) between post-pre ITC values and post-pre variability of taps. Dark blue regions represent no significance. B, Scatter plot between change in performance variability (SD) and change in ITC, averaged over significant electrodes shown in A.

have improved timing abilities (Repp, 2010). However, in most cases, these musicians have undergone many years of formal training, with many of them starting their training from early childhood. In this study, we demonstrated that, even with a smaller duration of musical rhythm training (2 months) at late-stages of life, age-related declines in temporal attention can be remediated. Furthermore, these results show that rhythmic timing ability remains plastic throughout the lifespan and dampens the concern that musicians are a self-selected group because of their inherent timing abilities. Rather, the choice to pursue musical training may stem from differences in self-concept (Demorest et al., 2017) or motivation (McAuley et al., 2011).

The improvement in temporal attention was neurally reflected by an increase in  $\delta$  band ITC from pre- to post-training. Because ITC is a measure of phase consistency across trials,





**Figure 7.** Slices show axial (top row) and sagittal (bottom row) views of source localized  $\delta$  band ITC in the Rhythmicity group during the slow tempo.

the correlation between ITC and performance indicates that more consistent neural activity patterns are related to more consistent synchronization performance. Notably, ITC was found to increase in anticipation of stimulus onset, as well as post stimulus onset. This indicates that increased ITC cannot be simply be attributed to changes in stimulus-evoked phase resetting, which would otherwise suggest a change in sensory processing. Rather, the increased  $\delta$  band ITC more likely reflects temporal attention processes that underlie the timing aspects of motor planning. Indeed, prior research has shown that low-frequency  $\delta$  band (1–4 Hz) oscillatory brain activity is phase synchronized with the temporal pattern of an external rhythm, which in turn facilitates the prediction of target stimuli (Lakatos et al., 2008; Schroeder and Lakatos, 2009). Importantly,  $\delta$  band activity, particularly its phase synchronization, has been increasingly associated with exogenous temporal attention ability (Stefanics et al., 2010; Gomez-Ramirez et al., 2011; Cravo et al., 2013; Arnal et al., 2015; Wilsch et al., 2015; Arnal and Kleinschmidt, 2017; Breska and Deouell, 2017) and this  $\delta$  phase synchronization may be influenced by cerebellar activity (Breska and Ivry, 2020). In previous studies, neural entrainment to external rhythmic activity has been shown to be a mechanism of enhanced processing efficiency (Schroeder and Lakatos, 2009; Zion Golumbic et al., 2013; Kayser et al., 2015; Lakatos et al., 2016). Here, we suggest such processing efficiency is related to temporal attention, which in turn, may affect sensory or motor-based processes.

Source localization of the brain regions associated with the increased  $\delta$  ITC show significant changes in premotor cortex, anterior cingulate cortex, inferior parietal lobule, and postcentral gyrus from pre- to post-training. Although previous studies have localized, these results are in general agreement with previous fMRI research assessing neural regions associated with temporal attention (Coull and Nobre, 2008). The premotor cortex is known to be involved in motor planning (Hoshi and Tanji, 2006; Nakayama et al., 2008; Li et al., 2016). It is critically involved in rhythm production (Halsband et al., 1993) and is associated with the processing and perception of rhythmic stimuli, such as speech (Meister et al., 2007; Kotz

and Schwartz, 2010). Conversely, the anterior cingulate cortex is associated with error detection and correction (Carter et al., 1998; Kiehl et al., 2000; Garavan et al., 2002; Swick and Turken, 2002; Veen and van Carter, 2002), such as needed during rhythmic synchronization tasks (Jantzen et al., 2018). On the other hand, the inferior parietal lobule has been associated with tasks involving temporal predictions, including synchronization tasks (Janata and Grafton, 2003; Pecenka et al., 2013; Andreou et al., 2015; De Pretto and James, 2015). Interestingly, the inferior parietal lobule has also been associated with motor intentions, motor predictions, and the feeling of “wanting to move” (Rizzolatti et al., 2006; Desmurget and Sirigu, 2012). Similar to the inferior parietal lobule, the postcentral gyrus has been linked to temporal predictions (Andreou et al., 2015; Jantzen et al., 2018), but it is also associated with somatosensory processing (Nelson and Chen, 2008) and is commonly observed in synchronization

tasks (Chauvigné et al., 2014). Together, our findings suggest that the source localized areas for  $\delta$  ITC contributed to temporal attention processes through temporal predictions in conjunction with error detection and correcting for timing deviations during the synchronization task. Importantly, the regions identified as being involved in temporal attention are commonly associated with the sensorimotor network (Stephan et al., 2002; Jantzen et al., 2007; Bueti et al., 2008; Anwar et al., 2016). Given that sensory and motoric processes were not affected by rhythm training, these results indicate the sensorimotor network is involved in critical timing functions (i.e., temporal attention) needed for sensorimotor synchronization. This is in line with the Action Simulation for Auditory Prediction hypothesis, which suggests that motor planning regions provide essential timing information to help predict upcoming beats (Patel and Iversen, 2014).

In this study, we also assessed whether improvements in exogenous temporal attention (orienting attention to external stimuli for timing information) transferred to endogenous temporal attention (orienting attention internally for timing information). However, we did not find any such supporting evidence. This lack of transfer supports models that suggest timing is a distributed process that may rely on modality- or context-specific neural regions (for review, see Mauk and Buonomano, 2004; Ivry and Schlerf, 2008; Paton and Buonomano, 2018). Temporal attention abilities improve in accordance with the networks that are most often engaged (Janzen et al., 2014). As such, if our musical rhythm training paradigm had included a component that taxed endogenous temporal attention ability, it likely would have improved performance on our endogenous temporal attention task. In support of this notion, research has shown that musical training in older adults that focused on endogenous temporal attention (solo piano performance) has shown improved endogenous timing ability as measured via continuation tapping, but not exogenous timing as indexed by synchronization tapping (Fujioka and Ross, 2017). Thus, improvement in one form of timing ability will not necessarily transfer to the other.



These results are in agreement with mounting evidence that cognitive interventions generally do not improve untrained cognitive domains (Simons et al., 2016; Swaminathan and Schellenberg, 2021). Rather, transfers of benefit from cognitive interventions are often observed in tasks that may be different from the trained task but use the same cognitive function. It has been long debated whether learned behaviors can be applied to novel contexts (Singley and Anderson, 1989). It has also been suggested that the content of what can be transferred can be classified along three dimensions: (1) procedure, representation, and principles are transferred during learned skills; (2) speed, accuracy, and approach are transferred during performance change; and (3) execution, recognition, and recall are transferred during memory demands (Barnett and Ceci, 2002). Transfer is most likely to occur when the training has been offered on generalized principles, when outcome measures are similar to that of the trained tasks and when it requires minimal memory retrieval from the trained task (Barnett and Ceci, 2002; Zelinski, 2009). Although we did not observe transfer between exogenous and endogenous temporal attention abilities, this is not to say that learned timing abilities do not transfer within exogenous or within endogenous temporal attention tasks. Indeed, training on tasks that rely on endogenous temporal attention has shown transfer within modality such that the stimuli used during training to encode the timing interval can change within modality and still yield comparable benefits in timing. This has been observed when changing auditory features (Wright et al., 1997), somatosensory (skin) locations (Nagarajan et al., 1998), or visual fields (Westheimer, 1999). Transfer within endogenous temporal attention tasks has also been observed across modalities, including from somatosensory to auditory (Nagarajan et al., 1998), from visual to auditory (Buetti et al., 2012), and from auditory to visual (Bartolo and Merchant, 2009). Moreover, even perceptual training can improve motor timing (Planetta and Servos, 2008; Meegan et al., 2000). Thus, transfer of learned timing abilities may certainly occur within specific constraints.

Yet, such transfer within endogenous temporal attention tasks is not always observed (Grondin and Ulrich, 2011). This is particularly true when it comes to the specific duration of the trained interval, as transfer to other interval durations is not common (Buetti and Buonomano, 2014). Interestingly, this may help explain why the Rhythmicity group exhibited improvements specifically at the slow and medium tempos in the exogenous temporal attention task because the training took place largely at tempos similar to the slow and medium tempos of the task. If true, the prediction would be that participants who trained at a fast tempo would exhibit improvements during the fast tempo of the exogenous temporal attention task. Unfortunately, we cannot test this with the current data because participants did not train long enough to reach performance levels that would enable training at a tempo that is comparable to the fast tempo of the exogenous temporal attention task. Through extensive pilot testing, we observed that only musicians (10+ years of training) were able to reach Rhythmicity levels that required performance at comparably fast tempos (i.e., 350 ms intertap interval).

A potential limitation of this study is that it was conducted in healthy older, not younger, adults. It could be argued that a lack of transfer to the endogenous temporal attention task may reflect age-related changes in brain function that are not specifically linked to a potential generalized neural mechanism of timing. For example, in the endogenous temporal attention task, neither

group of participants benefitted from predictive cues before or after training. Therefore, it could be argued that a lack of transfer to the endogenous temporal attention task arose from an age-related change in strategy where older adults did not attempt to use temporal attention to boost performance, thereby eliminating any possible benefits of transfer. However, we have previously demonstrated that this lack of benefit in performance is not indicative of a strategy shift that abandons temporal attention as older adults modulate anticipatory neural activity that indexes temporal attention, but to a lesser extent compared with young adults (Zanto et al., 2011). Moreover, in our assessment of exogenous temporal attention, we showed that the training-related improvements in performance were driven by the on-beat task, which has the most reliance on exogenous temporal attention. The off-beat (syncopation) and continuation tasks did not exhibit as large of a training effect, likely because these tasks include some aspects of endogenous temporal attention. This provides additional (albeit less direct) assessments of endogenous temporal attention, further supporting the idea that exogenous and endogenous temporal attention relies on distinct neural mechanisms. Thus, it seems unlikely that age played a role in the lack of transfer because a common neural mechanism should be equally affected by age regardless of task.

In conclusion, in this study, our aim was to understand if and how rhythm training can improve temporal attention in a healthy aging population. A group of nonmusician older adults performed a rhythm training task, and another group of nonmusician older adults completed an active control task. The group that received rhythm training showed significant improvement in their exogenous temporal attention abilities, as indexed by decreased variability in task performance. Moreover, rhythm training increased intertrial phase coherence (ITC), which correlated with improved performance. Further analysis localized these changes in ITC to a sensorimotor network, including premotor cortex, anterior cingulate cortex, postcentral gyrus, and inferior parietal lobule. These regions have been previously found to be associated with motor planning, error detection, and temporal predictions. Together, these results support the hypothesis that musical rhythm training can remediate age-related declines in exogenous temporal attention, which occurs via alterations in  $\delta$  phase coherence within a sensorimotor network. However, no evidence was found indicating a transfer of benefit from exogenous to endogenous temporal attention abilities, providing support for separate neural mechanisms underlying these subtypes of temporal attention.

## References

- Andreou LV, Griffiths TD, Chait M (2015) Sensitivity to the temporal structure of rapid sound sequences: an MEG study. *Neuroimage* 110:194–204.
- Androulidakis AG, Doyle LM, Yarrow K, Litvak V, Gilbertson TP, Brown P (2007) Anticipatory changes in beta synchrony in the human corticospinal system and associated improvements in task performance. *Eur J Neurosci* 25:3758–3765.
- Anguera JA, Boccanfuso J, Rintoul JL, Al-Hashimi O, Faraji F, Janowich J, Kong E, Larraburo Y, Rolle C, Johnston E, Gazzaley A (2013) Video game training enhances cognitive control in older adults. *Nature* 501:97–101.
- Anwar AR, Muthalib M, Perrey S, Galka A, Granert O, Wolff S, Heute U, Deuschl G, Raethjen J, Muthuraman M (2016) Effective connectivity of cortical sensorimotor networks during finger movement tasks: a simultaneous fNIRS, fMRI, EEG study. *Brain Topogr* 29:645–660.
- Arnal LH, Kleinschmidt AK (2017) Entrained delta oscillations reflect the subjective tracking of time. *Commun Integr Biol* 10:e1349583.

- Arnal LH, Doelling KB, Poeppel D (2015) Delta–beta coupled oscillations underlie temporal prediction accuracy. *Cereb Cortex* 25:3077–3085.
- Barnett SM, Ceci SJ (2002) When and where do we apply what we learn? A taxonomy for far transfer. *Psychol Bull* 128:612–637.
- Bartolo R, Merchant H (2009) Learning and generalization of time production in humans: rules of transfer across modalities and interval durations. *Exp Brain Res* 197:91–100.
- Bollinger J, Rubens MT, Masangkay E, Kalkstein J, Gazzaley A (2011) An expectation-based memory deficit in aging. *Neuropsychologia* 49:1466–1475.
- Bouwer FL, Honing H, Slagter HA (2020) Beat-based and memory-based temporal expectations in rhythm: similar perceptual effects, different underlying mechanisms. *J Cogn Neurosci* 32:1221–1241.
- Breska A, Deouell LY (2014) Automatic bias of temporal expectations following temporally regular input independently of high-level temporal expectation. *J Cogn Neurosci* 26:1555–1571.
- Breska A, Deouell LY (2017) Neural mechanisms of rhythm-based temporal prediction: delta phase-locking reflects temporal predictability but not rhythmic entrainment. *PLoS Biol* 15:e2001665.
- Breska A, Ivry RB (2018) Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson's disease. *Proc Natl Acad Sci USA* 115:12283–12288.
- Breska A, Ivry RB (2020) Context-specific control over the neural dynamics of temporal attention by the human cerebellum. *Sci Adv* 6:eabb1141.
- Bueti D, Buonomano DV (2014) Temporal perceptual learning. *Timing Time Percept* 2:261–289.
- Bueti D, Walsh V, Frith C, Rees G (2008) Different brain circuits underlie motor and perceptual representations of temporal intervals. *J Cogn Neurosci* 20:204–214.
- Bueti D, Lasaponara S, Cercignani M, Macaluso E (2012) Learning about time: plastic changes and interindividual brain differences. *Neuron* 75:725–737.
- Cameron DJ, Grahn JA (2014) Enhanced timing abilities in percussionists generalize to rhythms without a musical beat. *Front Hum Neurosci* 8:1003.
- Carter CS, Braver TS, Barch DM, Botvinick MM, Noll DC, Cohen JD (1998) Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280:747–749.
- Chauvigné LA, Gitau KM, Brown S (2014) The neural basis of audiomotor entrainment: an ALE meta-analysis. *Front Hum Neurosci* 8:776.
- Cope TE, Grube M, Singh B, Burn DJ, Griffiths TD (2014) The basal ganglia in perceptual timing: timing performance in multiple system atrophy and Huntington's disease. *Neuropsychologia* 52:73–81.
- Coull JT, Nobre AC (1998) Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J Neurosci* 18:7426–7435.
- Coull JT, Nobre AC (2008) Dissociating explicit timing from temporal expectation with fMRI. *Curr Opin Neurobiol* 18:137–144.
- Cravo AM, Rohenkohl G, Santos KM, Nobre AC (2017) Temporal anticipation based on memory. *J Cogn Neurosci* 29:2081–2089.
- Cravo AM, Rohenkohl G, Wyart V, Nobre AC (2013) Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. *J Neurosci* 33:4002–4010.
- de Diego-Balaguer R, Martinez-Alvarez A, Pons F (2016) Temporal attention as a scaffold for language development. *Front Psychol* 7:44.
- De Pretto M, James C (2015) Principles of parsimony: fMRI correlates of beat-based versus duration-based sensorimotor synchronization. *Psychomusicology: Music, Mind, and Brain* 25:380–391.
- Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 134:9–21.
- Demorest SM, Kelley J, Pfordresher PQ (2017) Singing ability, musical self-concept, and future music participation. *J Res Music Educ* 64:405–420.
- Desmurget M, Sirigu A (2012) Conscious motor intention emerges in the inferior parietal lobule. *Curr Opin Neurobiol* 22:1004–1011.
- Franěk M, Mates J, Radil T, Beck K, Pöppel E (1991) Finger tapping in musicians and nonmusicians. *Int J Psychophysiol* 11:277–279.
- Fujioka T, Ross B (2017) Beta-band oscillations during passive listening to metronome sounds reflect improved timing representation after short-term musical training in healthy older adults. *Eur J Neurosci* 46:2339–2354.
- Fujioka T, Trainor LJ, Large EW, Ross B (2009) Beta and gamma rhythms in human auditory cortex during musical beat processing. *Ann NY Acad Sci* 1169:89–92.
- Garavan H, Ross TJ, Murphy K, Roche RA, Stein EA (2002) Dissociable executive functions in the dynamic control of behavior: inhibition, error detection, and correction. *Neuroimage* 17:1820–1829.
- Gomez-Ramirez M, Kelly SP, Molholm S, Sehatpour P, Schwartz TH, Foxe JJ (2011) Oscillatory sensory selection mechanisms during intersensory attention to rhythmic auditory and visual inputs: a human electrocorticographic investigation. *J Neurosci* 31:18556–18567.
- Graber E, Fujioka T (2020) Induced beta power modulations during isochronous auditory beats reflect intentional anticipation before gradual tempo changes. *Sci Rep* 10:4207.
- Grondin S, Ulrich R (2011) Duration discrimination performance: no cross-modal transfer from audition to vision even after massive perceptual learning. In: *Multidisciplinary aspects of time and time perception* (Vatakis A, Esposito A, Giagkou M, Cummins F, Papadelis G, eds), pp 92–100. New York: Springer.
- Halsband U, Ito N, Tanji J, Freund HJ (1993) The role of premotor cortex and the supplementary motor area in the temporal control of movement in man. *Brain* 116:243–266.
- Hoshi E, Tanji J (2006) Differential involvement of neurons in the dorsal and ventral premotor cortex during processing of visual signals for action planning. *J Neurophysiol* 95:3596–3616.
- Ivry RB, Schlerf JE (2008) Dedicated and intrinsic models of time perception. *Trends Cogn Sci* 12:273–280.
- Ivry RB, Spencer RM, Zelaznik HN, Diedrichsen J (2002) The cerebellum and event timing. *Ann NY Acad Sci* 978:302–317.
- Janata P, Grafton ST (2003) Swinging in the brain: shared neural substrates for behaviors related to sequencing and music. *Nat Neurosci* 6:682–687.
- Jantzen KJ, Oullier O, Marshall M, Steinberg FL, Kelso JA (2007) A parametric fMRI investigation of context effects in sensorimotor timing and coordination. *Neuropsychologia* 45:673–684.
- Jantzen KJ, Ratcliff BR, Jantzen MG (2018) Cortical networks for correcting errors in sensorimotor synchronization depend on the direction of asynchrony. *J Mot Behav* 50:235–248.
- Janzen TB, Thompson WF, Ammirante P, Ranvaud R (2014) Timing skills and expertise: discrete and continuous timed movements among musicians and athletes. *Front Psychol* 5:1482.
- Kayser SJ, Ince RA, Gross J, Kayser C (2015) Irregular speech rate dissociates auditory cortical entrainment, evoked responses, and frontal alpha. *J Neurosci* 35:14691–14701.
- Kiehl KA, Liddle PF, Hopfinger JB (2000) Error processing and the rostral anterior cingulate: an event-related fMRI study. *Psychophysiology* 33:282–294.
- Kotz SA, Schwartze M (2010) Cortical speech processing unplugged: a timely subcortico-cortical framework. *Trends Cogn Sci* 14:392–399.
- Lakatos P, Karmos G, Mehta AD, Ulbert I, Schroeder CE (2008) Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* 320:110–113.
- Lakatos P, Barczak A, Neymotin SA, McGinnis T, Ross D, Javitt DC, O'Connell MN (2016) Global dynamics of selective attention and its lapses in primary auditory cortex. *Nat Neurosci* 19:1707–1717.
- Large EW, Jones MR (1999) The dynamics of attending: how we track time-varying events. *Psychol Rev* 106:119–159.
- Li N, Daie K, Svoboda K, Druckmann S (2016) Robust neuronal dynamics in premotor cortex during motor planning. *Nature* 532:459–464.
- Makeig S (1993) Auditory event-related dynamics of the EEG spectrum and effects of exposure to tones. *Electroencephalogr Clin Neurophysiol* 86:283–293.
- Mauk MD, Buonomano DV (2004) The neural basis of temporal processing. *Annu Rev Neurosci* 27:307–340.
- McAuley JD, Jones MR (2003) Modeling effects of rhythmic context on perceived duration: a comparison of interval and entrainment approaches to short-interval timing. *J Exp Psychol Hum Percept Perform* 29:1102–1125.
- McAuley JD, Jones MR, Holub S, Johnston HM, Miller NS (2006) The time of our lives: life span development of timing and event tracking. *J Exp Psychol* 135:348–367.
- McAuley JD, Henry MJ, Tuft S (2011) Musician advantages in music perception: an issue of motivation: not just ability. *Music Percept* 28:505–518.

- Meegan DV, Aslin RN, Jacobs RA (2000) Motor timing learned without motor training. *Nat Neurosci* 3:860–862.
- Meister IG, Wilson SM, Deblieck C, Wu AD, Iacoboni M (2007) The essential role of premotor cortex in speech perception. *Curr Biol* 17:1692–1696.
- Miall C (1989) The storage of time intervals using oscillating neurons. *Neural Comput* 1:359–371.
- Mishra J, de Villers-Sidani E, Merzenich M, Gazzaley A (2014) Adaptive training diminishes distractibility in aging across species. *Neuron* 84:1091–1103.
- Mishra J, Anguera JA, Gazzaley A (2016) Video games for neuro-cognitive optimization. *Neuron* 90:214–218.
- Morillon B, Baillet S (2017) Motor origin of temporal predictions in auditory attention. *Proc Natl Acad Sci USA* 114:E8913–E8921.
- Nagarajan SS, Blake DT, Wright BA, Byl N, Merzenich MM (1998) Practice-related improvements in somatosensory interval discrimination are temporally specific but generalize across skin location, hemisphere, and modality. *J Neurosci* 18:1559–1570.
- Nakayama Y, Yamagata T, Tanji J, Hoshi E (2008) Transformation of a virtual action plan into a motor plan in the premotor cortex. *J Neurosci* 28:10287–10297.
- Nelson AJ, Chen R (2008) Digit somatotopy within cortical areas of the post-central gyrus in humans. *Cereb Cortex* 18:2341–2351.
- Nobre AC, van Ede F (2018) Anticipated moments: temporal structure in attention. *Nat Rev Neurosci* 19:34–48.
- Olson IR, Chun MM (2001) Temporal contextual cuing of visual attention. *J Exp Psychol* 27:1299–1313.
- Padgaonkar NA, Zanto TP, Bollinger J, Gazzaley A (2017) Predictive cues and age-related declines in working memory performance. *Neurobiol Aging* 49:31–39.
- Pashler H (2001) Perception and production of brief durations: beat-based versus interval-based timing. *J Exp Psychol* 27:485–493.
- Pascual-Marqui RD (2002) Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. *Methods Find Exp Clin Pharmacol* 24(Suppl. D):5–12.
- Patel AD, Iversen JR (2014) The evolutionary neuroscience of musical beat perception: the Action Simulation for Auditory Prediction (ASAP) hypothesis. *Front Syst Neurosci* 8:57.
- Paton JJ, Buonomano DV (2018) The neural basis of timing: distributed mechanisms for diverse functions. *Neuron* 98:687–705.
- Pecenkova N, Engel A, Keller P (2013) Neural correlates of auditory temporal predictions during sensorimotor synchronization. *Front Hum Neurosci* 7:380.
- Planetta PJ, Servos P (2008) Somatosensory temporal discrimination learning generalizes to motor interval production. *Brain Res* 1233:51–57.
- Praamstra P, Kourtis D, Kwok HF, Oostenveld R (2006) Neurophysiology of implicit timing in serial choice reaction-time performance. *J Neurosci* 26:5448–5455.
- Rammesayer TH, Buttkus F, Altenmüller E (2012) Musicians do better than nonmusicians in both auditory and visual timing tasks. *Music Percept* 30:85–96.
- Repp BH (2010) Sensorimotor synchronization and perception of timing: effects music training and task experience. *Hum Mov Sci* 29:200–213.
- Repp BH, Iversen JR, Patel AD (2008) Tracking an imposed beat within a metrical grid. *Music Percept* 26:1–18.
- Rizzolatti G, Ferrari PF, Rozzi S, Fogassi L (2006) The inferior parietal lobule: where action becomes perception. *Novartis Found Symp* 270:129–140; discussion 140–145, 164–169.
- Rohenkohl G, Nobre AC (2011) Alpha oscillations related to anticipatory attention follow temporal expectations. *J Neurosci* 31:14076–14084.
- Rohenkohl G, Coull JT, Nobre AC (2011) Behavioural dissociation between exogenous and endogenous temporal orienting of attention. *PLoS One* 6:e14620.
- Schroeder CE, Lakatos P (2009) Low-frequency neuronal oscillations as instruments of sensory selection. *Trends Neurosci* 32:9–18.
- Simons DJ, Boot WR, Charness N, Gathercole SE, Chabris CF, Hambrick DZ, Stine-Morrow EA (2016) Do “brain-training” programs work? *Psychol Sci Public Interest* 17:103–186.
- Singley MK, Anderson JR (1989) *The transfer of cognitive skill*. Cambridge, MA: Harvard UP.
- Snyder JS, Large EW (2005) Gamma-band activity reflects the metric structure of rhythmic tone sequences. *Cogn Brain Res* 24:117–126.
- Spencer RM, Ivry RB, Zelaznik HN (2005) Role of the cerebellum in movements: control of timing or movement transitions? *Exp Brain Res* 161:383–396.
- Spencer RM, Verstynen T, Brett M, Ivry R (2007) Cerebellar activation during discrete and not continuous timed movements: an fMRI study. *Neuroimage* 36:378–387.
- Stefanics G, Hangya B, Hernádi I, Winkler I, Lakatos P, Ulbert I (2010) Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. *J Neurosci* 30:13578–13585.
- Stephan KM, Thaut MH, Wunderlich G, Schicks W, Tian B, Tellmann L, Schmitz T, Herzog H, McIntosh GC, Seitz RJ, Hömberg V (2002) Conscious and subconscious sensorimotor synchronization: prefrontal cortex and the influence of awareness. *Neuroimage* 15:345–352.
- Swaminathan S, Schellenberg EG (2021) Music training. In: *Cognitive training: an overview of features and applications* (Strobach T, Karbach J, eds), pp 307–318. New York: Springer.
- Swick D, Turken AU (2002) Dissociation between conflict detection and error monitoring in the human anterior cingulate cortex. *Proc Natl Acad Sci USA* 99:16354–16359.
- Teghil A, Boccia M, D’Antonio F, Di Vita A, de Lena C, Guariglia C (2019) Neural substrates of internally-based and externally-cued timing: an activation likelihood estimation (ALE) meta-analysis of fMRI studies. *Neurosci Biobehav Rev* 96:197–209.
- Teke S, Grube M, Kumar S, Griffiths TD (2011) Distinct neural substrates of duration-based and beat-based auditory timing. *J Neurosci* 31:3805–3812.
- Teke S, Grube M, Griffiths T (2012) A unified model of time perception accounts for duration-based and beat-based timing mechanisms. *Front Integr Neurosci* 5:90.
- Todorovic A, Schoffelen JM, Ede F, van Maris E, Lange F (2015) Temporal expectation and attention jointly modulate auditory oscillatory activity in the beta band. *PLoS One* 10:e0120288.
- Treisman M (1963) Temporal discrimination and the indifference interval: implications for a model of the ‘internal clock.’ *Psychol Monogr* 77:1–31.
- Veen V, van Carter CS (2002) The timing of action-monitoring processes in the anterior cingulate cortex. *J Cogn Neurosci* 14:593–602.
- Westheimer G (1999) Discrimination of short time intervals by the human observer. *Exp Brain Res* 129:121–126.
- Wilsch A, Henry MJ, Herrmann B, Maess B, Obleser J (2015) Slow-delta phase concentration marks improved temporal expectations based on the passage of time. *Psychophysiology* 52:910–918.
- Wright BA, Buonomano DV, Mahncke HW, Merzenich MM (1997) Learning and generalization of auditory temporal-interval discrimination in humans. *J Neurosci* 17:3956–3963.
- Zanto TP, Large EW, Fuchs A, Kelso JA (2005) Gamma-band responses to perturbed auditory sequences: evidence for synchronization of perceptual processes. *Music Percept* 22:531–547.
- Zanto TP, Hennigan K, Östberg M, Clapp WC, Gazzaley A (2010) Predictive knowledge of stimulus relevance does not influence top-down suppression of irrelevant information in older adults. *Cortex* 46:564–574.
- Zanto TP, Pan P, Liu H, Bollinger J, Nobre AC, Gazzaley A (2011) Age-related changes in orienting attention in time. *J Neurosci* 31:12461–12470.
- Zanto TP, Padgaonkar NT, Nourishad A, Gazzaley A (2019) A tablet-based assessment of rhythmic ability. *Front Psychol* 10:2471.
- Zanto TP, Liu H, Pan P, Gazzaley A (2020) Temporal attention is not affected by working memory load. *Cortex* 130:351–361.
- Zanto TP, Johnson V, Ostrand A, Gazzaley A (2022) How musical rhythm training improves short term memory for faces. *PNAS* 119:e2201655119.
- Zelinski EM (2009) Far transfer in cognitive training of older adults. *Restor Neurol Neurosci* 27:455–471.
- Ziegler DA, Simon AJ, Gallen CL, Skinner S, Janowich JR, Volponi JJ, Rolle CE, Mishra J, Kornfield J, Anguera JA, Gazzaley A (2019) Closed-loop digital meditation improves sustained attention in young adults. *Nat Hum Behav* 3:746–757.
- Zion Golumbic EM, Ding N, Bickel S, Lakatos P, Schevon CA, McKhann GM, Goodman RR, Emerson R, Mehta AD, Simon JZ, Poeppel D, Schroeder CE (2013) Mechanisms underlying selective neuronal tracking of attended speech at a ‘cocktail party.’ *Neuron* 77:980–991.