

COGNITIVE NEUROSCIENCE

Getting back on the beat: links between auditory–motor integration and precise auditory processing at fast time scales

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Abstract

The auditory system is unique in its ability to precisely detect the timing of perceptual events and use this information to update motor plans, a skill that is crucial for language. However, the characteristics of the auditory system that enable this temporal precision are only beginning to be understood. Previous work has shown that participants who can tap consistently to a metronome have neural responses to sound with greater phase coherence from trial to trial. We hypothesized that this relationship is driven by a link between the updating of motor output by auditory feedback and neural precision. Moreover, we hypothesized that neural phase coherence at both fast time scales (reflecting subcortical processing) and slow time scales (reflecting cortical processing) would be linked to auditory–motor timing integration. To test these hypotheses, we asked participants to synchronize to a pacing stimulus, and then changed either the tempo or the timing of the stimulus to assess whether they could rapidly adapt. Participants who could rapidly and accurately resume synchronization had neural responses to sound with greater phase coherence. However, this precise timing was limited to the time scale of 10 ms (100 Hz) or faster; neural phase coherence at slower time scales was unrelated to performance on this task. Auditory–motor adaptation therefore specifically depends upon consistent auditory processing at fast, but not slow, time scales.

Introduction

The auditory system precisely tracks the timing of perceptual events and coordinates this information with the motor system. Studies of synchronized tapping, for example, have shown that participants are less variable when tapping to an auditory beat than when tapping to a visual beat (Kolers & Brewster, 1985; Chen *et al.*, 2002; Patel *et al.*, 2005; Hove *et al.*, 2013). This precise auditory–motor integration may also be important for auditory perception, as listeners may categorize speech sounds and track temporal patterns by mapping acoustic information onto articulatory gestures (Kotz & Schwartze, 2010; Schulze *et al.*, 2012; Peelle & Davis, 2012). However, little is known about the mechanisms that make this auditory–motor precision possible.

One way to investigate the neural foundations of precise auditory–motor timing integration is to examine individual differences among

participants. Participants whose frequency-following neural responses to sound show greater phase coherence from trial to trial tap more consistently to a beat (Tierney & Kraus, 2013) and are better able to read (Hornickel & Kraus, 2013). This suggests that, to perform auditory–motor temporal integration, whether when acquiring language skills or when performing a non-linguistic rhythm task, the auditory system must consistently represent the timing of sounds on a millisecond-level time scale. However, synchronizing to a metronome is a complex process consisting of several components, including the production of steady movement, reliable internal time-keeping, and adaptation to changes in the timing relationship between sound and movement (Semjen *et al.*, 1998; Thaut *et al.*, 1998). It remains unknown, therefore, which of these components relies upon consistent auditory processing. In particular, it remains to be demonstrated that auditory–motor integration is specifically linked to auditory neural precision. We hypothesized that auditory neural temporal precision is vital for auditory–motor temporal integration. To test this hypothesis, we predicted that millisecond-level auditory neural phase coherence would be linked to the ability to adapt to small shifts in the timing of sound events during synchronization.

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Another open question is how auditory–motor temporal integration depends on neural precision at different time scales. Previous work reported a relationship between the precision of high-frequency auditory responses (10 ms and faster) and synchronization performance (Tierney & Kraus, 2013). Neural precision at time scales of 10 ms and faster (≥ 100 Hz) may be particularly vital, because the sound-to-movement alignment errors that arise during synchronization occur at the level of a few milliseconds. Precision at slower time scales, however, may also be important, given that low-frequency neural entrainment tracks the rhythmic structure of sound sequences (Large, 2008; Nozaradan *et al.*, 2011, 2012; Tierney & Kraus, 2014). Given an emerging view of the auditory system as a distributed, but integrated, neural circuit (Kraus & White-Schwoch, 2015), we hypothesized that neural precision across both slow and fast time scales is important for accurate auditory time perception. To test this hypothesis, we predicted that phase coherence across multiple time scales would be linked to auditory–motor temporal integration ability. Here, we investigated the neural correlates of auditory–motor timing integration skill by asking participants to synchronize to a metronome that changed either its tempo or its timing. Neural responses to speech were collected to determine how temporal adaptation ability related to neural phase coherence at the faster time scale of the frequency-following response (≤ 10 ms, corresponding to ≥ 100 Hz) and the slower time scale of the evoked cortical response (100–200 ms, corresponding to 5–10 Hz).

Materials and methods

Subjects

Sixty-five participants (31 females) were recruited from local high schools and universities. The mean age of participants was 18.10 years (standard deviation, 0.98). Participants had no diagnosis of a learning or neurological disorder, and had normal hearing thresholds of < 20 dB (with regard to normal hearing level) for octaves between 250 Hz and 8000 Hz. Click-evoked auditory brainstem response latencies were within normal limits, as established by our laboratory (5.41–5.97 ms; 100- μ s click stimulus presented at 80 dB SPL at a rate of 31/s). For participants aged < 18 years, informed assent was obtained from the participant and consent was obtained from the participant's legal guardian. Informed consent was obtained for all participants aged > 18 years. All procedures were approved by the Institutional Review Board at Northwestern University.

Drumming

Apparatus

Stimuli for the synchronization tests were created in MATLAB (The Mathworks), stored on an iPod Nano (Apple), and presented over headphones. The drum sound used in both tests was a 150-ms recording of a struck conga drum acquired at freesound.org. Participants listened to the stimulus track while drumming on a conga drum with a drum trigger (Pulse Percussion) placed against the underside of the drum head. The output of the drum trigger was combined with a copy of the auditory signal being presented to the participant as two channels of a stereo input to a computer running the audio recording program AUDACITY. Thus, the timing relationship between the stimulus input and the participant's drumming was captured in real time.

Processing

Drumming data were processed by a custom-made program that took as input the audio file created in AUDACITY, and returned a list of stimulus presentation and drum onset times. Continuous variations in amplitude were transformed into discrete onsets by setting an amplitude threshold and a relaxation time. Time points were marked as onsets if: (i) the amplitude of the point exceeded the amplitude threshold; and (ii) a length of time equal to or greater than the relaxation time had passed since the last time point when the threshold was exceeded. Amplitude thresholds and relaxation times were set manually on a subject-by-subject basis to account for inter-individual variation in the exact manner in which the drum was struck. Drum and stimulus onsets were checked by visually comparing a vector of onset times with the raw amplitude contour, to ensure that all onsets were correctly marked and that all marked onsets corresponded to a drum or stimulus onset. These stimulus and drum onsets were then subjected to further processing to produce the summary scores for each test, as described below.

Tempo adaptation test

This test measured participants' ability to rapidly adapt to a shift in a metronome's tempo. Participants were presented with 55 trials. Each trial consisted of between 11 and 15 presentations of a conga drum sound. In each trial, the first 6–10 sounds were separated by 500-ms intervals. During five of the 55 trials, the last five sound presentations continued at the same rate. The other 50 trials included a tempo shift: in 25 of the trials, the stimulus rate was switched to a slower tempo for the last five sound presentations, with five trials each using tempos of 550, 540, 530, 520 and 510 ms. In the remaining 25 trials, the stimulus rate switched to a faster tempo for the last five presentations, with five trials each using tempos of 450, 460, 470, 480 and 490 ms. Condition order was pseudorandomized so that both the degree and direction of the tempo shift (i.e. faster or slower) were unpredictable. This test lasted for ~ 10 min.

Participants were asked to drum along to the beat. They were told that, at some point, the drum beat might change to a new tempo, and that, if they heard a tempo shift, they should switch the tempo of their drumming to match the new drum tempo. Performance was assessed for each trial by measuring the difference between the target tempo and each of the last two intervals produced. For example, if a given trial's target tempo was 460 ms and the last two intervals that the participant produced were 450 ms and 480 ms, the participant's score for that trial would be $(10 + 20)/2$ or 15. Lower scores indicated better performance.

Timing shift adaptation test

This test measured participants' ability to resume synchronization with a metronome after a single metronome interval was lengthened or shortened. A total of four trials were presented to the participants. During each trial, participants heard a conga sound presented with a constant inter-stimulus interval of 500 ms, and were asked to synchronize to the beat. Participants were told that one of the sounds might occasionally sound as though it were off of the beat, but that they should do their best to keep their movements in time with the sounds that they were hearing. Occasionally, a single interval was either lengthened or shortened. Each trial contained a total of 16 shifted beats that were separated by eight isochronous beats to give

the participant time to resume synchronization. In two of the four trials, the interval was lengthened or shortened by 10 ms, and in the remaining two trials, the interval was lengthened or shortened by 50 ms. Order of presentation of lengthened vs. shortened intervals was pseudorandomized so that the direction of the shift was unpredictable.

This single altered time interval increased the offset between the participants' drumming and the stimulus. To minimize this offset, participants needed to resynchronize to the beat. This test therefore provides an efficient way to assess participants' ability to rapidly synchronize. The degree of synchronization following an altered metronome interval was quantified as the standard deviation of the offset between the participant's movements and the drum sound onset for the six beats following the shifted interval. Performance was averaged across all four trials. Lower scores indicated better performance.

Electrophysiology

Stimulus and recording

The stimulus for the neurophysiological testing was a 170-ms 'da' synthesized with a Klatt synthesizer. The stimulus consisted of a 5-ms onset burst followed by a 45-ms consonant–vowel transition period followed by a 120-ms steady-state vowel period. From 5 ms to 50 ms, the fundamental frequency stayed constant at 100 Hz, the first formant increased from 400 Hz to 720 Hz, the second formant decreased from 1700 Hz to 1240 Hz, and the third formant decreased from 2580 Hz to 2500 Hz. From 50 ms to 170 ms, the fundamental frequency remained constant at 100 Hz, while the first, second and third formants stayed constant at 720, 1240 and 2500 Hz, respectively. The fourth, fifth and sixth formants stayed constant from 5 ms to 170 ms at 3300, 3750 and 4900 Hz, respectively. Stimuli were presented with Neuroscan Stim² (Compumedics) at 80 dB SPL at a rate of 3.95 Hz through insert earphones (ER-3; Etymotic Research). Stimuli were presented in alternating polarities; adding neural responses to alternating polarities ensured that the neural measures described below were not contaminated by stimulus artefacts. Presenting stimuli in alternating polarities is a standard way of accentuating both the phase coherence and amplitude of the fundamental frequency response, as adding the alternate polarities accentuates the lower-frequency response envelope, and subtracting the polarities accentuates the higher-frequency fine structure (Aiken & Picton, 2008). Electrophysiological data were collected with NEUROSCAN ACQUIRE 4.3. A montage of three Ag–AgCl electrodes was used, with the active electrode at Cz, ground at the forehead, and reference at the right earlobe. All impedances were kept below 5 k Ω , with inter-electrode differences kept below 3 k Ω . Data were digitally sampled at 20 000 Hz. During the recording session, participants sat quietly while watching a movie to maintain a state of calm alertness. Six thousand artefact-free trials were collected (3000 of each polarity).

Stimuli were presented in two different conditions. In the quiet condition, stimuli were presented in the absence of background noise. A noise condition was also used to determine whether stressing the auditory system via background noise would elicit a wider range of inter-subject phase-locking, potentially strengthening links between neural function and auditory–motor precision. In the noise condition, therefore, stimuli were presented in the context of multi-talker background babble at a signal-to-noise ratio of +10 dB relative to the root-mean-square amplitude of the noise. Both stimulus and noise were presented monaurally to the right ear.

Electroencephalography data processing

The phase coherence of the neural response to sound was examined by calculating inter-trial phase-locking. Raw neural data were epoched from –40 ms to 250 ms around stimulus onset. Trials with amplitudes exceeding 35 μ V were rejected as artefacts. Epochs were baseline corrected to the mean amplitude of the epoch and detrended, and the first and final 15 ms of each epoch were ramped with a Hann window. A set of complex Morlet wavelets was then convoluted with each response trial at each time point, providing a measure of the amplitude and phase for each time \times frequency bin. To analyse the inter-trial phase-locking of the frequency-following response, complex Morlet wavelets with centre frequencies of 70–410 Hz in 1-Hz steps were used, with the bandwidth parameter set as 6.5 Hz. (Setting the bandwidth parameter to a constant value results in a constant window duration being applied across frequencies.) To analyse the inter-trial phase-locking of the low-frequency evoked response, wavelets with centre frequencies of 1–50 Hz in 1-Hz steps were used, with the bandwidth parameter set as 0.5 Hz. Amplitude provides a measure of the amount of energy present in the signal at that frequency, and phase provides an estimate of the timing of the response at that frequency. Averaging normalized phase vectors across trials and then calculating the length of the resulting vector therefore gives a measure of the extent to which the response varies in phase at that time \times frequency point. A phase-locking value of 1 would indicate perfect inter-trial synchrony, whereas a small phase-locking value would indicate no inter-trial neural synchrony. Phase-locking data were displayed in 3D colour plots (Fig. 2). For statistical analysis, frequency-following response phase-locking was quantified as average phase-locking in 20-Hz bins centred around the fundamental frequency and the first through third harmonics (100, 200, 300 and 400 Hz) from 5 ms to 170 ms. Visual analysis revealed that phase-locking below 50 Hz was primarily limited to the high theta range (5–10 Hz). Low-frequency evoked response phase-locking was therefore calculated as average phase-locking between 5 Hz and 10 Hz from 5 ms to 170 ms.

As a confirmatory measure, the consistency of the neural response was also calculated (Hornickel *et al.*, 2012). First, raw continuous data were band-passed by the use of one of two pass bands: low-frequency (1–50 Hz) or high-frequency (70–2000 Hz). Data were then epoched from –40 ms to 210 ms, and trials with amplitude exceeding ± 35 μ V were rejected as artefacts. Epochs were then baselined to the amplitude of the prestimulus period. A total of 6000 artefact-free trials were analysed. A random sampling process was repeated 300 times to produce an estimate of the average consistency between responses to the stimulus. For each sample, 3000 randomly selected trials were averaged, and then the remaining 3000 trials were combined to form a second average. The portions of these two waveforms between 5 ms and 170 ms after sound onset were then correlated. A response that is more consistent from trial to trial will lead to highly similar subaverages and a more robust correlation, whereas more variability from trial to trial will lead to dissimilar subaverages and a weaker correlation. Finally, the 300 resulting *r*-values produced by this process were averaged and converted to a *z*-score via a Fisher transform to create a global response consistency score.

Processed data are available on the Open Science Framework at <https://osf.io/xgshh/>. These data include performance on the tempo and timing adaptation tests, and response consistency and inter-trial phase-locking for neural responses to sounds presented in quiet and noise.

Statistical analysis

To confirm that the relationship between phase-locking and auditory-motor adaptation held across all tempo shift conditions, a repeated measures ANOVA was performed, with phase-locking group (top vs. bottom third) as the between-subjects factor, tempo shift condition as the within-subjects factor, and adaptation performance as the dependent variable. To determine whether the addition of noise impacted the relationship between auditory-motor adaptation ability and inter-trial phase coherence, a series of repeated measures ANOVAs were performed, with drumming performance group as the between-subjects variable (top vs. bottom third of performers) and stimulus presentation condition (quiet vs. noise) as the within-subjects variable. Separate ANOVAs were performed for the timing shift vs. tempo adaptation tests and for high-frequency vs. low-frequency phase-locking, giving a total of four ANOVAs.

The following data were normally distributed, and were therefore not transformed: composite data for the period correction and timing shift correction tests, and high-frequency and low-frequency phase-locking in quiet and noise. Response consistency data, however, were not normally distributed, and outliers of greater than two standard deviations away from the mean were therefore removed to achieve normality. The critical phase locking value at $P = 0.05$ was calculated as 0.02234 from the estimation of the circular mean described in Fisher (1996). Six subjects showed frequency-following response phase-locking values for the fundamental frequency through the fourth harmonic (100, 200, 300 and 400 Hz) that were not significant according to this analysis, and were excluded from our main analysis.

To determine the relationship between auditory-motor integration ability and neural precision, four stepwise linear regressions were performed. In one, low-frequency evoked and frequency-following response phase coherence were included as possible predictors of tempo adaptation. In another, low-frequency vs. high-frequency phase coherence predicted phase adaptation. In the remaining two, low-frequency and high-frequency response consistency predicted tempo and phase adaptation. Follow-up Spearman correlational analyses were performed, comparing performance on each synchronization test with composite phase-locking at high and low frequencies averaged across quiet and noise conditions, and with composite response consistency of responses band-passed with low-pass and high-pass bands. Spearman correlational analyses were used to further investigate relationships between inter-trial phase-locking, response consistency, and adaptation ability. Correlation confidence intervals (CIs) were calculated with the method of Bonett & Wright (2000).

Results

There was no interaction between phase-locking group and tempo shift ($F_{1,42} = 1.61$, $P = 0.149$), confirming that the degree of shift did not affect the relationship between auditory-motor adaptation and neural phase consistency. Similarly, for timing shifts, there was no interaction between phase-locking group and degree of shift ($F_{1,42} = 2.01$, $P = 0.129$). Therefore we collapsed across all tempo and timing shift conditions prior to our main analysis.

Participants showed greater phase-locking in response to sounds presented in quiet than in response to sounds presented in noise (main effect of recording condition: quiet vs. noise, $F_{1,42} = 42.85$, $P < 0.001$). However, the extent to which phase-locking was enhanced in the participants who were better able to perform tempo adaptation did not differ between the quiet and noise conditions (no

interaction between group and recording condition, $F_{1,42} = 0.260$, $P = 0.613$). Similarly, for the timing shift adaptation test, the extent to which phase-locking was enhanced in the good adapters as compared with the poor adapters did not differ between quiet and noise conditions (no interaction between group and recording condition, $F_{1,42} = 1.272$, $P = 0.266$). For the analyses in the remainder of the article, therefore, we produced composite measures by averaging phase coherence and response consistency across quiet and noise conditions.

Auditory-motor adaptation and phase coherence

Figure 1 shows a histogram of phase coherence across the fundamental frequency through the third harmonic (not including the six subjects who were excluded because they had phase coherence values falling below the critical value). Across responses to speech presented in both quiet and noise, inter-trial phase-locking at frequencies corresponding to the fundamental frequency and the first three harmonics of the stimulus (90–110, 190–210, 290–310 and 390–410 Hz) was higher in participants who were better at adapting to perturbation while synchronizing (Fig. 2, left; Figs 3 and 4). However, across responses to speech presented in both quiet and noise, inter-trial phase-locking at lower frequencies (5–10 Hz) was not linked to the ability to adapt to perturbation while synchronizing (Fig. 2, right; Fig. 3). Stepwise linear regression revealed that high-frequency phase coherence predicted tempo adaptation performance [$B = -187.457$ (CI -297.329 to -77.584), $R^2 = 0.170$, $P = 0.001$], but low-frequency phase coherence did not significantly improve the model ($P = 0.694$). Similarly, high-frequency phase coherence predicted timing shift adaptation performance [$B = -151.229$ (CI -254.223 to -48.234), $R^2 = 0.132$, $P = 0.005$], but low-frequency phase coherence did not significantly improve the model ($P = 0.783$).

Auditory-motor adaptation and response consistency

Across responses to speech presented in both quiet and noise, the consistency of the response filtered at frequencies corresponding to the frequency-following response (70–2000 Hz) was higher in participants who were better at adapting to perturbation while synchronizing (Fig. 5). However, across responses to speech presented in both quiet and noise, the consistency of the response filtered at frequencies corresponding to the evoked response (1–50 Hz) was not linked to the ability to adapt to perturbation while synchronizing.

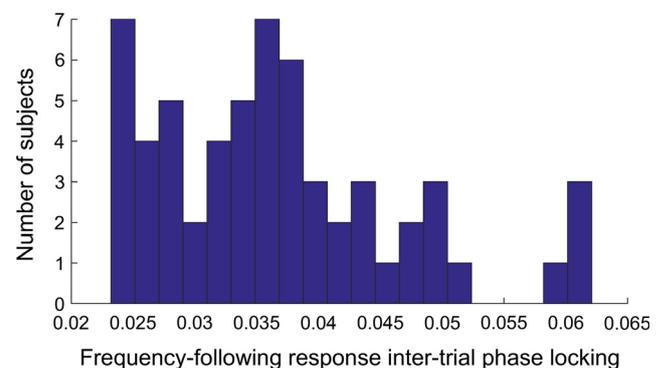


FIG. 1. Inter-trial phase-locking across subjects: histogram of degree of inter-trial phase locking averaged across 20-Hz bins centred on the fundamental frequency and the first three harmonics (100, 200, 300 and 400 Hz).

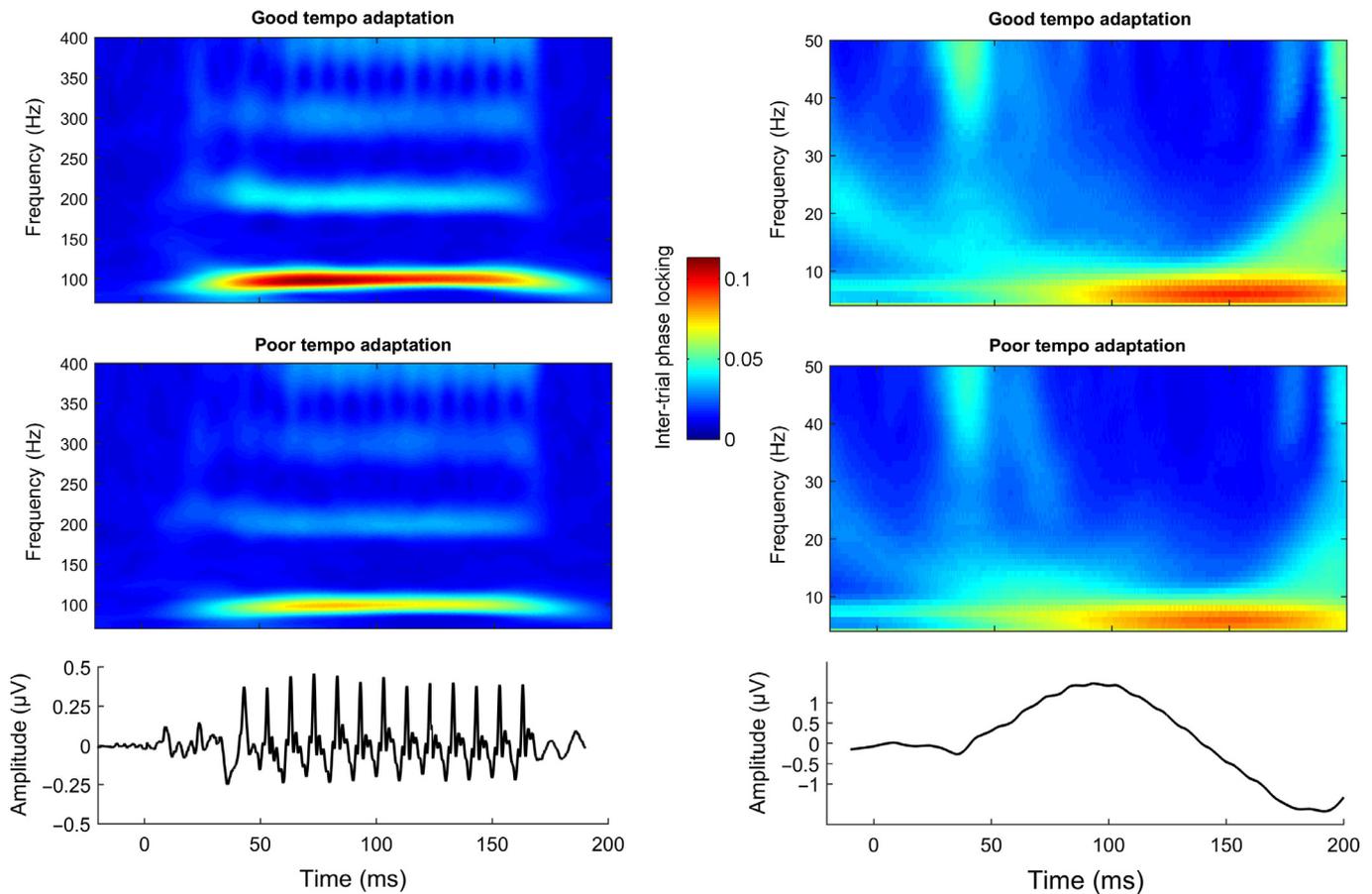


FIG. 2. Inter-trial phase locking and tempo adaptation performance. Upper left: inter-trial phase-locking at ≥ 70 Hz in participants who performed better vs. those who performed worse on a test of tempo adaptation (top vs. bottom third of performers). Upper right: inter-trial phase-locking at ≤ 50 Hz in participants who showed good vs. poor tempo adaptation performance. Bottom left: grand average response across all subjects high-pass filtered at 70 Hz. Bottom right: grand average response low-pass filtered at 50 Hz. Responses displayed in the bottom two panels are a composite of average responses to speech sounds presented in quiet and in background noise. Critical phase-locking values were 0.0223 for $P = 0.05$ as calculated with the method of Bonett & Wright (2000). Grand averages were calculated by taking the mean of the absolute values of the complex individual values.

Stepwise linear regression revealed that frequency-following response consistency predicted tempo adaptation performance [$B = -10.157$ (CI -15.612 to -4.703), $R^2 = 0.219$, $P < 0.001$], but low-frequency evoked response consistency did not significantly improve the model ($P = 0.716$). Similarly, frequency-following response consistency tended to predict timing shift adaptation performance [$B = -4.774$ (CI -10.392 to 0.845), $R^2 = 0.055$, $P = 0.094$], but low-frequency evoked response consistency did not significantly improve the model ($P = 0.817$).

Correlational analyses

Correlational analyses were used to further investigate relationships between inter-trial phase-locking, response consistency, and adaptation ability (Figs 5–7). Given the lack of an interaction between group and recording condition in the analyses reported above, a composite phase-locking score was generated by averaging values for the quiet and noise responses. Subjects who performed better on the tempo adaptation task had stronger phase-locking ($\rho = -0.416$, $P = 0.001$, CI -0.614 to -0.168) and response consistency ($\rho = -0.447$, $P < 0.001$, CI -0.643 to -0.196) at the frequencies characterizing the frequency-following response, but did not show an advantage for phase-locking ($\rho = 0.068$, $P = 0.608$, CI -0.192 to 0.319) or response consistency ($\rho = -0.021$,

$P = 0.881$, CI -0.248 to 0.287) at the lower frequencies that make up the evoked response. Similarly, phase adaptation tracked with phase-locking ($\rho = -0.343$, $P = 0.008$, CI -0.556 to -0.088) and response consistency ($\rho = -0.270$, $P = 0.044$, CI -0.500 to -0.002) at the frequencies characterizing the frequency-following response, but did not track with phase-locking ($\rho = 0.059$, $P = 0.658$, CI -0.200 to 0.311) or response consistency ($\rho = 0.045$, $P = 0.745$, CI -0.226 to 0.309) at the lower frequencies that make up the evoked response. Tempo and timing shift adaptation were correlated (Fig. 6; $\rho = 0.477$, $P < 0.001$, CI 0.238 – 0.662). Finally, inter-trial phase-locking of the frequency-following response was not correlated with phase-locking of the low-frequency evoked response ($\rho = 0.067$, $P = 0.614$, CI -0.193 to 0.318).

Discussion

As predicted, participants who were better able to rapidly adapt to a changing metronome tempo or more quickly resynchronized to a beat after a timing shift had neural responses with greater phase coherence from trial to trial. However, in contrast to our predictions, this greater neural precision was limited to the higher frequencies that make up the subcortical frequency-following response (90–410 Hz, corresponding to time scales of 2.5–11 ms). Good and

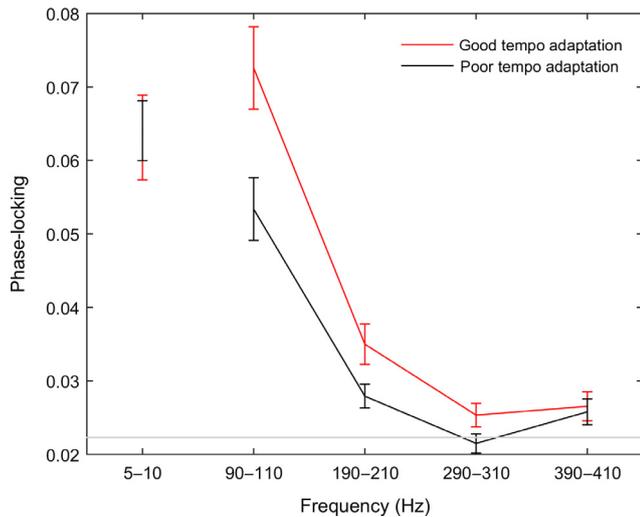


FIG. 3. Inter-trial phase-locking and tempo adaptation performance: mean phase-locking values (composite score across both quiet and noise stimulus presentation conditions) for the participants who were better (red) vs. those who were worse (black) at quickly adapting to a change in metronome tempo (top vs. bottom third of performers). Behavioural performance was calculated as the absolute difference between the timing shift present in the stimulus and the timing shift produced by the participant. Error bars indicate one standard error of the mean. The light grey horizontal line indicates the critical value (0.0223) for significant phase-locking at $P = 0.05$.

poor adapters did not differ in neural precision at the lower frequencies that characterize the cortical evoked response (5–10 Hz, or 100–200 ms).

Humans can accurately synchronize to sound by rapidly and precisely adapting to errors that emerge from transient fluctuations in stimulus input and motor output (Repp, 2000; Madison & Merker, 2004). However, not everyone is equally skilled at this auditory–motor integration, and we predicted that the phase coherence of neural

sound processing across slow and fast time scales would help to determine error correction skill. As predicted, we found that participants whose frequency-following responses to sound showed greater phase coherence from trial to trial were better able to adapt to timing shifts while synchronizing. However, in contrast to our predictions, we found that the phase coherence of the lower-frequency cortical response was unrelated to auditory–motor adaptation skills. These results suggest that auditory neural precision on the time scale of ≥ 100 Hz (periods of ≤ 10 ms) that characterizes the frequency-following response is crucial for accurate auditory–motor temporal integration. Auditory neural precision on the slower scale of 5–10 Hz (100–200 ms) that characterizes the cortical response, however, does not seem to underlie accurate auditory–motor adaptation. It may instead be more important for tasks that require the integration of auditory information over time, such as extraction of the beat from a complex stimulus or encoding a sequence of durations into memory, a prediction that could be investigated by future work.

We previously reported (Tierney & Kraus, 2013) that variability during beat synchronization is lower in subjects with more precise frequency-following responses. However, beat synchronization is a complex task, and synchronization variability can therefore reflect different sources of variance, including motor variability, timekeeper variability, and the use of auditory feedback to correct transient increases in the asynchrony between movement and sound. Here, we present evidence that temporal precision of the frequency-following response is vital for auditory–motor timing integration. The primary neural generator of the frequency-following response (Chandrasekaran & Kraus, 2010) is the inferior colliculus (IC), a region that may play a crucial role in the auditory–motor error correction processes that make synchronization possible. The IC is a neural hub, receiving afferent input from peripheral auditory structures (Kudo & Niimi, 1980; Coleman & Clerici, 1987) and efferent input from cortical regions (Bajo *et al.*, 2010). The IC is also capable of precisely phase-locking to high-frequency auditory input (Liu *et al.*, 2006), a characteristic that causes it to be the primary

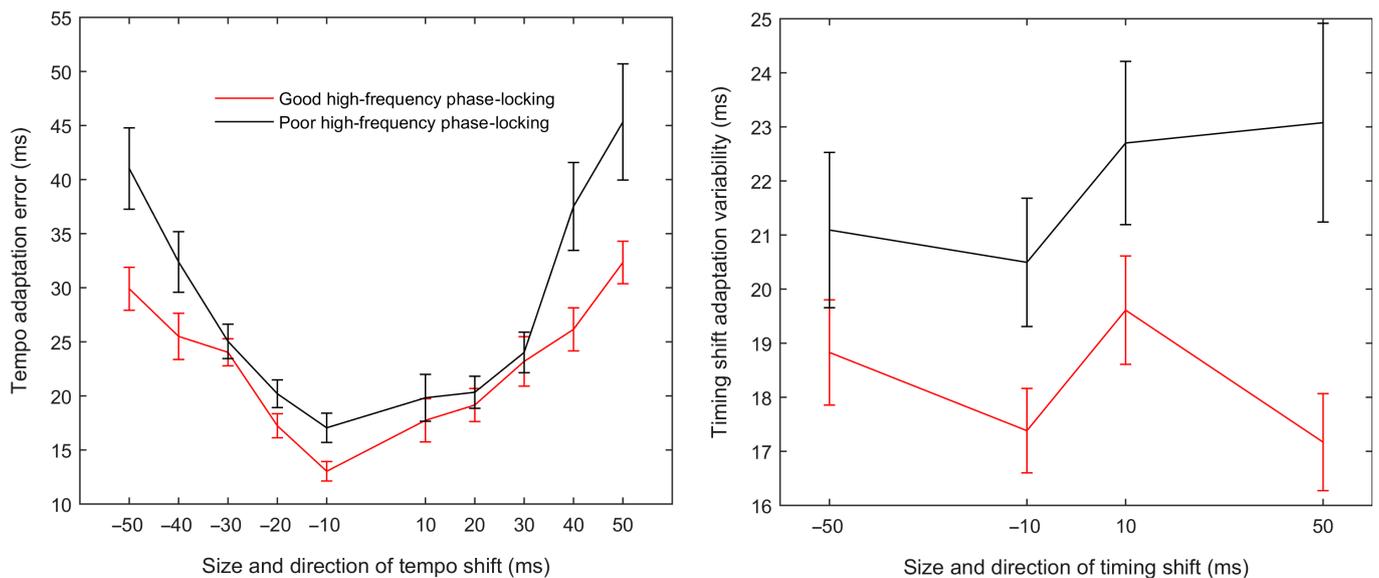


FIG. 4. Auditory–motor adaptation across conditions in participants with good vs. poor high-frequency phase-locking: tempo (left) and timing shift (right) adaptation performance across all conditions in participants with good vs. poor high-frequency phase-locking. Phase-locking was measured in 20-Hz bins centred on the fundamental frequency and the first three harmonics. Tempo adaptation performance was calculated as the absolute difference between the timing shift present in the stimulus and the timing shift produced by the participant. Timing adaptation performance was calculated as the standard deviation of the offset between the participant’s movements and the drum sound onset for the six beats following the lengthened or shortened stimulus interval.

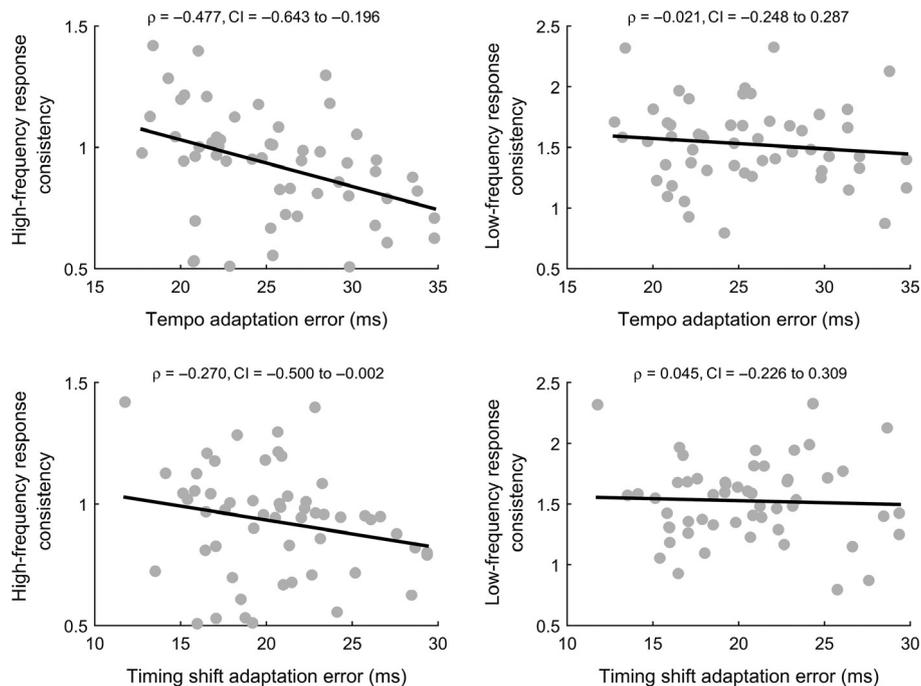


FIG. 5. Relationship between tempo and timing shift adaptation and response consistency. Top left: scatterplot of tempo adaptation error vs. frequency-following response consistency ($\rho = -0.477$, $P < 0.001$, CI -0.643 to -0.196). Top right: scatterplot of tempo adaptation error vs. low-frequency evoked response consistency ($\rho = -0.021$, $P = 0.881$, CI -0.248 to 0.287). These correlations were significantly different according to Meng's z -test ($z = 2.801$, $P = 0.003$). Bottom left: scatterplot of timing shift adaptation error vs. frequency-following response consistency ($\rho = -0.270$, $P = 0.044$, CI -0.500 to -0.002). Bottom right: scatterplot of timing shift adaptation error vs. low-frequency evoked response consistency ($\rho = 0.045$, $P = 0.745$, CI -0.226 to 0.309). These correlations were significantly different according to Meng's z -test ($z = 1.789$, $P = 0.037$). Timing adaptation performance was calculated as the standard deviation of the offset between the participant's movements and the drum sound onset for the six beats following the lengthened or shortened stimulus interval.

generator of the frequency-following response (Warrier *et al.*, 2011). Moreover, the IC connects directly to the cerebellum, bypassing the auditory cortex (Mower *et al.*, 1979; Hashikawa, 1983; Saint Marie, 1996). The cerebellum updates motor behaviour by comparing expected with actual feedback (Wolpert *et al.*, 1998), and is involved in both auditory-motor synchronization (Molinari *et al.*, 2007; Bijsterbosch *et al.*, 2011) and perceptual timing (Lee *et al.*, 2007). The cerebellum, in turn, connects to the basal ganglia, the proposed location of a beat-based timing system (Grahn and Brett, 2007; Teki *et al.* 2011, Bartolo *et al.*, 2014) that has been linked to a deficit in tempo adaptation (Schwartz *et al.* 2011). The IC's temporal precision, integrative role and direct connection to subcortical motor structures therefore make it ideal for communicating auditory timing information to motor regions (Molinari *et al.*, 2005; Warren *et al.*, 2005; Malcolm *et al.*, 2008), a process that is crucial for auditory-motor integration. Our results suggest that fine temporal precision in the IC is important for accurate auditory-motor integration. Thus, temporal precision in the auditory midbrain may be a crucial gatekeeper that helps to determine individual differences in auditory-motor timing ability.

On the other hand, the lack of relationships between phase-locking at slower time scales (100–200 ms) and adaptation to timing perturbation during synchronization suggests that low-frequency cortical temporal precision is not a crucial factor driving precise auditory-motor integration. This is surprising, given that cells in the premotor cortex are tuned to duration and serial order (Merchant *et al.*, 2013; Crowe *et al.* 2014), that the auditory cortex and motor/premotor cortex are functionally connected during synchronization tasks (Pollok *et al.*, 2003; Chen *et al.*, 2006, 2008; Krause *et al.*

2010), and that phase-locking of slow cortical oscillations plays a role in the tracking of rhythmic information (Nozaradan *et al.*, 2011, 2012; Tierney & Kraus, 2014). It is possible that the auditory cortex is responsible for integrating timing information over a longer time scale, on the order of hundreds of milliseconds or more, which would be more important for tasks such as remembering rhythmic sequences or predicting the timing of future rhythmic events (Merchant *et al.*, 2015) than for synchronization. Thus, although the auditory cortex and premotor cortex do interact during synchronization, slow auditory phase-locking may not be a bottleneck for synchronization skill, because beat synchronization does not rely on integration of information across time periods longer than tens of milliseconds. Alternatively, it could be that other cortical functions besides low-frequency phase-locking are important for error correction in synchronization. Perhaps, for example, subcortical high-frequency phase coherence can affect the temporal consistency of the middle latency response, which then influences synchronization via connections to the premotor cortex.

Another possible explanation for the lack of a connection between low-frequency neural phase coherence and synchronization adaptation is that the sounds to which participants were synchronizing were characterized by very rapid amplitude onsets. For sounds with gradually ramping onsets, amplitude rise time helps to determine perceived onset time (Caclin *et al.*, 2005). As tracking of the amplitude envelope is tied to phase-locking of slow cortical oscillations (Luo & Poeppel, 2007; Abrams *et al.*, 2008; Poeppel *et al.*, 2008; Abrams *et al.*, 2009; Goswami, 2011), it could be that synchronization to stimuli with less abrupt onsets (such as speech stimuli) depends more on slow-time-scale neural consistency. For stimuli

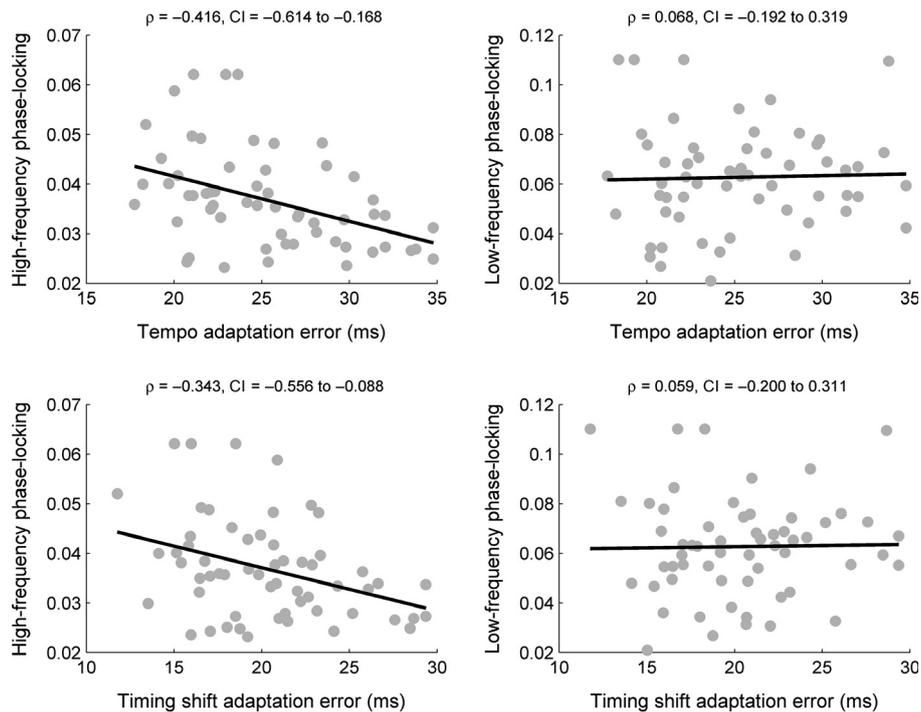


FIG. 6. Relationship between tempo and timing shift adaptation and inter-trial phase-locking. Top left: scatterplot of tempo adaptation error vs. inter-trial phase-locking measured in 20-Hz bins centred on the fundamental frequency and the first three harmonics ($\rho = -0.416$, $P = 0.001$, CI -0.614 to -0.168). Top right: scatterplot of tempo adaptation error vs. inter-trial phase-locking at 5–10 Hz ($\rho = 0.068$, $P = 0.608$, CI -0.192 to 0.319). These correlations were significantly different according to Meng's z -test ($z = 2.735$, $P = 0.003$). Bottom left: scatterplot of timing shift adaptation error vs. high-frequency inter-trial phase-locking ($\rho = -0.343$, $P = 0.008$, CI -0.556 to -0.088). Bottom right: scatterplot of timing shift adaptation error vs. inter-trial phase-locking at 5–10 Hz ($\rho = 0.059$, $P = 0.658$, CI -0.200 to 0.311). These correlations were significantly different according to Meng's z -test ($z = 0.246$, $P = 0.012$). Tempo adaptation performance was calculated as the absolute difference between the timing shift present in the stimulus and the timing shift produced by the participant.

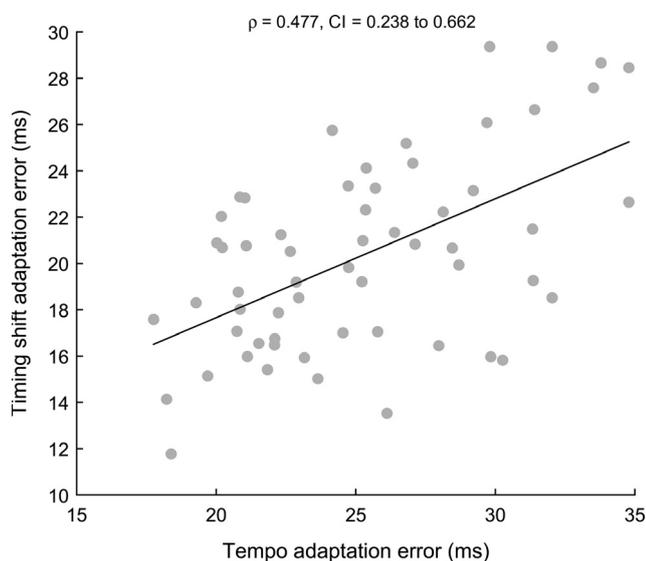


FIG. 7. Relationship between tempo adaptation and timing shift adaptation performance: scatterplot of tempo adaptation vs. timing shift adaptation error ($\rho = 0.477$, $P < 0.001$, CI 0.238 – 0.662). Phase-locking was measured in 20-Hz bins centred on the fundamental frequency and the first three harmonics. Tempo adaptation performance was calculated as the absolute difference between the timing shift present in the stimulus and the timing shift produced by the participant.

with abrupt onsets, on the other hand, the auditory system may instead be able to rely on the robust onset responses produced by subcortical auditory regions.

We found that inter-trial phase-locking of the frequency-following response and phase-locking of the lower-frequency cortical auditory evoked response were not correlated. This suggests that individual variations in phase coherence within the auditory system cannot be accounted for via a unitary mechanism. Instead, cortical and subcortical precision are decoupled, such that a given participant could have a precise low-frequency cortical response but an imprecise frequency-following response (or vice versa). Thus, a promising avenue for future research would be to investigate the mechanisms that determine neural precision at high and slow rates.

Although synchronization to an auditory beat is a skill that humans easily master, it is surprisingly rare in the animal kingdom, having been reported in only a handful of species to date (Patel *et al.*, 2009; Hasegawa *et al.*, 2011). Moreover, at present it has not been demonstrated in any other primate, despite at least one extensive attempt to teach the skill to rhesus monkeys (Zarco *et al.*, 2009). The majority of the species that have been shown to synchronize, including the African grey parrot and the sulphur-crested cockatoo, are capable of vocal learning (Patel *et al.*, 2009; Schachner *et al.*, 2009; although see Cook *et al.*, 2013), suggesting that there may be overlap between the auditory–motor connections that make vocal learning possible and those crucial for synchronization. Speculation to date regarding the necessary preconditions for synchronization has largely focused on connections between auditory cortical areas, premotor regions, and the basal ganglia (Patel *et al.*, 2009; Merchant & Honing, 2014; Patel & Iversen, 2014). However, our finding that high-frequency auditory neural precision (>100 Hz, corresponding to time scales of ≤ 10 ms) is linked to synchronization skill suggests that it may be fruitful to examine structural and functional interactions between subcortical auditory regions and motor

areas as well. For example, strengthening of the direct connection between the auditory midbrain and cerebellum could enable the rapid, precise auditory–motor integration necessary for both vocal learning and synchronization. Conversely, a lack of a strong connection between subcortical auditory and motor areas in species that cannot perform vocal learning could explain the lack of a benefit for auditory vs. visual stimuli for rhesus monkeys performing perceptual–motor synchronization tasks (Zarco *et al.*, 2009; Kraus & White-Schwoch, 2015).

Our finding that auditory neural precision at a fast time scale enables rapid adaptation during synchronization adds to the growing evidence that precision at fast time scales is crucial for auditory perception. Not only is neural precision linked to synchronization consistency (Tierney & Kraus, 2013) and adaptation, but children with more consistent frequency-following responses also perform better at word-reading tasks (Hornickel & Kraus, 2013). This suggests that a precise neural response enables extraction of a stable percept of the timing of sound and reliable categorization of speech sounds, whereas a less precise response interferes with these processes. Given that auditory neural precision appears to be important for the development of language skills and a gatekeeper for synchronization ability, it is an intriguing question whether synchronization training could enhance neural precision, potentially boosting language skills. Indirect support for this view is provided by studies of musical training, which have revealed that musical training tracks with enhanced consistency of neural responses to sound (Parbery-Clark *et al.*, 2012; Skoe & Kraus, 2013) and enhanced language skills (Moreno *et al.*, 2009; Parbery-Clark *et al.*, 2009; Kolinsky *et al.*, 2009; Bhide *et al.*, 2013; François *et al.*, 2013; Zuk *et al.*, 2013; Slater *et al.*, 2014). Moreover, short-term auditory training has been shown to enhance both response consistency and language skills (Hornickel *et al.*, 2012). Given that synchronization training via computer-based training programs would be cost-effective and efficient, examining the effects of synchronization training on neural function and language skill is a promising avenue for the future.

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Abbreviations

CI, confidence interval; IC, inferior colliculus.

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