



Hemispheric asymmetries in auditory temporal integration: A study of event-related potentials



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ABSTRACT

According to the asymmetric sampling in time hypothesis, the left auditory cortex processes stimuli using a short temporal integration window (~25–50 ms), whereas the right auditory cortex processes stimuli using a long temporal integration window (~200 ms). We examined N1 and T-complex responses to the second tone of tone-pairs presented with inter-stimulus intervals (ISIs) of 50 and 200 ms. Twenty-seven undergraduate students were presented with stimuli binaurally whilst the EEG was recorded. N1 and T_a responses were symmetric between hemispheres, with responses elicited by the second tone of the 50 ms ISI tone-pairs. T_b responses to the second tones were significantly attenuated over the right hemisphere when compared to the left hemisphere for the 50 ms ISI tone-pairs, but returned to similar amplitudes in the 200 ms condition. Our results suggest that temporal integration windows of the left and right primary auditory areas are symmetric whereas those of the left and right secondary auditory areas are asymmetric. These findings are consistent with the asymmetric sampling in time hypothesis and provide justification for further investigation of the involvement of temporal integration in higher order auditory processes.

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1. Introduction

1.1. Temporal integration windows in auditory processing

According to the asymmetric sampling in time hypothesis (Poehpel, 2003), observations of bilateral speech processing can be explained by applying an auditory processing framework that is based on differences in the temporal integration processes proposed to occur in each hemisphere. Temporal integration is the process by which temporally separated auditory signals are combined to form a unitary event; the temporally delimited period over which this occurs is referred to as a temporal integration window (Poehpel, 2003; Wang et al., 2005). The concept of a temporal integration window was first introduced by Stroud (1956) as the 'psychological moment'; the smallest perceivable segment of time that cannot be divided further. The concept is based on our discontinuous perception of time; we break the continuum of time into chunks and treat them as moments. The psychological moment is perceived as having a before and after, but no in-between; the temporal order of events occurring over

the period of a psychological moment cannot be perceived (Stroud, 1967). In a similar way, we segment the continuous stream of auditory information into chunks of information according to temporal integration windows, and treat them as unitary events. Poehpel (2003) suggested that there are at least two temporal integration windows of differing lengths (~25 ms and ~200 ms) by which we process auditory information. The neurons associated with each temporal integration window are distributed asymmetrically in the auditory cortices; this idea is referred to as the asymmetric sampling in time hypothesis.

A key concept of the asymmetric sampling in time hypothesis is that auditory signals are processed according to symmetrical temporal integration windows within the primary auditory cortices, but are then processed asymmetrically according to the different temporal integration windows within the secondary auditory cortices (Poehpel, 2003; Poehpel et al., 2008). Poehpel (2003) posited that a larger proportion of neurons in the left secondary auditory cortex function according to the short temporal integration window (~25–50 ms) and a larger proportion of neurons in the right secondary auditory cortex function according to a long temporal integration window (~200 ms). Poehpel (2003) proposed that the purpose of the short temporal integration window was for the processing of rapid modulations such as phonetic transitions (Poehpel, 2003; Poehpel et al., 1996), and the

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long temporal integration window was for the processing of slow modulations such as syllabic transitions and intonation (Luo and Poeppel, 2007). The asymmetry in the distribution of neurons associated with short and long temporal integration windows is suggested to be the basis for observed functional asymmetries (Poeppel, 2003).

1.2. Evidence for hemispheric asymmetries in auditory temporal integration

At present there is substantial evidence for the leftward lateralisation of activity for tasks associated with a short temporal integration window from a range of EEG, MEG, fMRI and PET studies (Belin et al., 1998; Brown and Nicholls, 1997; Jamison et al., 2006; Johnsrude et al., 1997; Liebenthal et al., 2005; Molfese, 1978; Nicholls, 1996; Nicholls et al., 2002; Okamoto et al., 2009; Poeppel et al., 1996; Zaehle et al., 2007; Zatorre and Belin, 2001; Zatorre et al., 1992). Studies demonstrating the rightward lateralisation of slow temporal processing, whilst increasing in number, are numerous. The most compelling findings come from fMRI, MEG and EEG studies.

Jamison et al. (2006) observed that the left hemisphere is more sensitive than the right hemisphere to increases in temporal variation of nonspeech stimuli using fMRI. Participants were presented with sequences of tones that alternated between 500 and 1000 Hz, and varied in duration. In the standard condition, the shortest tone with the highest probability was 667 ms. In the temporal condition, the shortest tone with the highest probability was 21 ms, making the temporal rate of alternation between tones faster than in the standard condition. Haemodynamic responses were spread over a significantly larger area in the left hemisphere than in the right hemisphere, suggesting that the left hemisphere may be specialised for the processing of rapid auditory signals.

Boemio et al. (2005) used fMRI to examine the sensitivity of the left and right auditory areas to variations in segmental structure. They used concatenated sequences of narrow-band noise segments. The mean duration of the segments within each sequence were 12, 25, 45, 85, 160 or 300 ms. Both hemispheres were sensitive to segment structure, however the processing of slowly modulated stimuli (300 ms) was lateralised to the secondary auditory cortex of the right hemisphere.

fMRI studies like those discussed above are useful for the localization of particular neural processes, due to the high spatial resolution afforded by the technique. However, the use of fMRI is limited in the study of temporal processing due to its poor temporal resolution. Therefore the investigation of the rapid changes in neural activity that are presumed to be involved in temporal auditory processing is limited. Even though two regions may be activated during a particular task, there may be differences in the neural processes occurring within each area that are not detectable using fMRI.

MEG, although lacking in spatial resolution available through fMRI, provides the high temporal resolution of neural activity that is required for investigating neural processes involved in the processing of temporal structure. Poeppel et al. (1996) used MEG to investigate hemispheric asymmetries in the M100 response to CV syllable pairs /bæ/ and /pæ/, and /dæ/ and /tæ/. Participants were presented with the stimuli passively and were not required to attend to them. In the active condition, participants were instructed to distinguish between the syllable-pairs, which only varied on voice-onset time (20 ms or 80 ms). The M100 responses to passively presented stimuli were bilaterally symmetric, but responses to stimuli during the active task increased over the left hemisphere and decreased over the right hemisphere.

As the temporal integration window has been suggested to correspond to the neuronal oscillations in the brain, researchers

have investigated the asymmetric sampling in time hypothesis using the analysis of gamma (40 Hz) and theta (4–8 Hz) oscillatory frequency bands. Luo and Poeppel (2012) examined phase-tracking responses to non-speech auditory stimuli using MEG. The stimuli were composed of frequency-modulated segments that were 25, 80, and 200 ms. They found that reliable phase-tracking of the stimulus modulations occurred for the 25 and 200 ms stimuli, but not the 80 ms stimuli, supporting the view that there are at least two timescales relevant to the processing of temporal structure. Phase tracking of the 25 ms (40 Hz) segment stimuli was observed bilaterally; however phase-tracking of the 200 ms (5 Hz) segment stimuli was lateralized to the right hemisphere. The study was unable to provide evidence of leftward bias for rapid acoustic transitions, however the results are consistent with the proposition that there is a rightward bias for slow acoustic transitions.

Although MEG has good temporal resolution, the technique is not sensitive to radially-oriented dipoles. The lack of sensitivity is problematic as there are neural components elicited by auditory stimuli that have radially oriented dipoles (detectable using EEG), and these components may provide relevant information regarding the hypotheses being tested. To avoid the temporal limitations of fMRI and the lack of sensitivity to radially-oriented dipoles of MEG, the present study uses EEG. EEG has the advantage of high temporal resolution, and is sensitive to both tangential and radial dipoles associated with ERP components elicited by auditory stimuli.

Many of the previously mentioned studies use tasks that involve either rapid (e.g. phonetic discrimination) or slow (e.g. sentence comprehension) temporal processes and infer the involvement of either the short or long temporal integration window. Using such complex stimuli can complicate the resulting patterns of asymmetry and does not provide clear associations between temporal processes and hemispheres of interest. Therefore, we have chosen to use a simple paired-tone paradigm to minimise the complexity of the stimuli and in turn, the interpretability of the resulting patterns of activity.

1.3. Event-related potential indices of auditory processing

The aim of the present study was to investigate whether auditory areas in the left and right hemispheres integrate acoustic stimuli according to different temporal integration windows using simple paired-tone stimuli. We used EEG to examine the cortical responses to tones, as indexed by event-related potentials (ERPs), and to determine whether there are differences in the time periods over which the left and right auditory cortices integrate auditory stimuli.

The N1 and T-complex (Ta and Tb) are peaks in the ERP waveform elicited by auditory stimuli (Näätänen and Picton, 1987; Wolpaw and Penry, 1975). The N1 is a widely studied measure of auditory signal processing in adults that has been used to examine hemispheric differences in auditory processing (Johnson et al., 2013; Näätänen and Picton, 1987; Okamoto et al., 2009; Poeppel et al., 1996). It is a negative deflection that occurs approximately 100 ms post-stimulus onset and is observed maximally at fronto-central sites (see Figs. 1 and 2).

The T-complex refers to two peaks, which are observed maximally at the temporal sites; a positive deflection at 105–110 ms post-stimulus onset (named the Ta) and a negative deflection (Tb) at 150–160 ms post-stimulus onset (see Figs. 1 and 2; Wolpaw and Penry, 1975). The T-complex is a less widely studied auditory ERP in adults as its amplitude reduces with age (Tonnuquist-Uhlen et al., 2003). The T-complex has a radially-oriented dipole, which can only be detected using EEG (Bishop et al., 2011). Previous studies have investigated the lateralisation of the T-complex response and its association with language impairments, such as dyslexia and

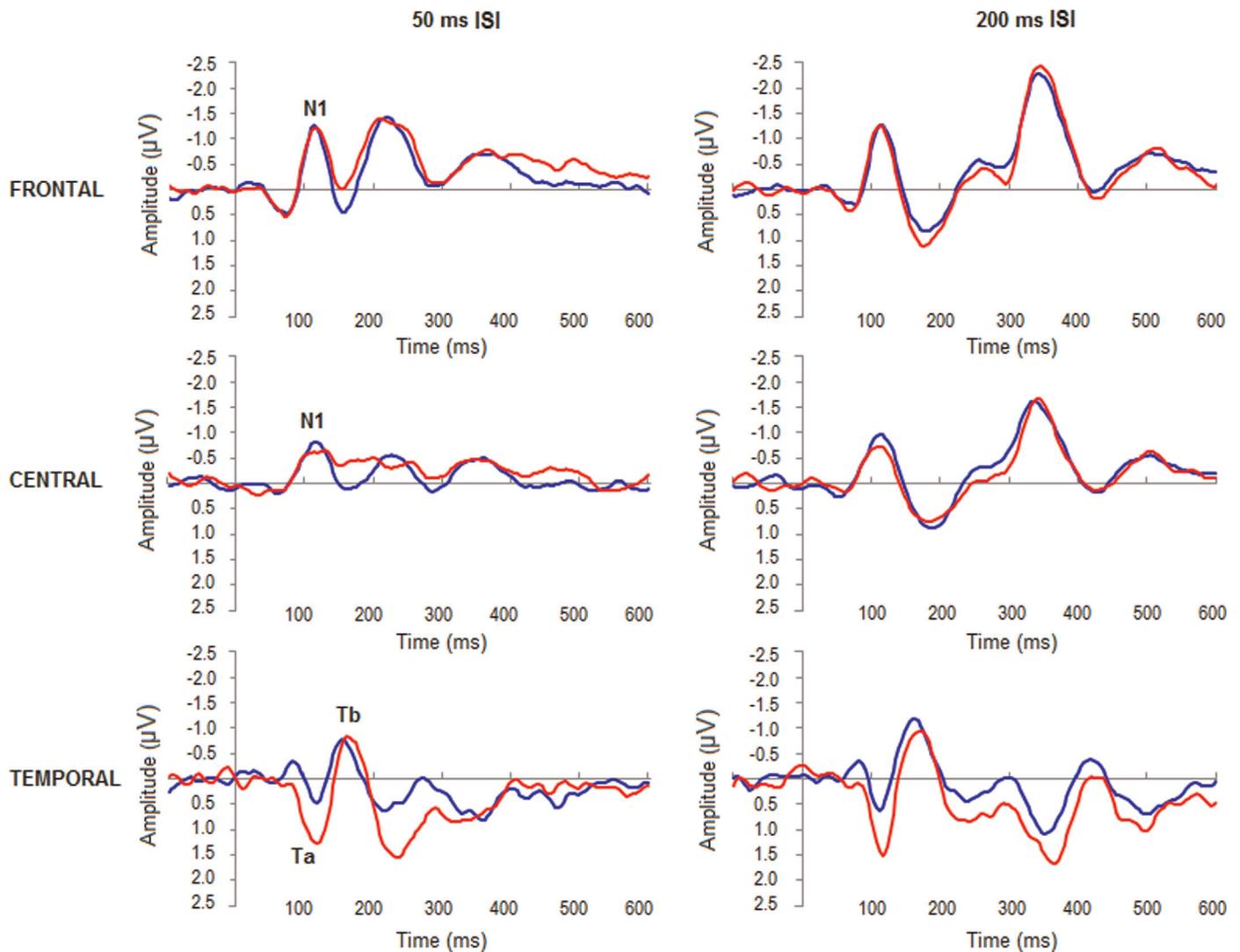


Fig. 1. Grand-averaged waveforms elicited in response to the first and second tone of tone pairs presented at ISIs of 50 ms and 200 ms. The amplitudes of the waveforms elicited over the left (blue/black) and right (red/grey) hemispheres at frontal, central, and temporal sites are given in microvolts (μV).

specific language impairment in adults and children (Bishop et al., 2012; Johnson et al., 2013; Shafer et al., 2011).

Our hypotheses are based on the notion that if two tones are separated by an interval shorter than the critical temporal integration window of the hemisphere of interest, the tones will be integrated and only one electrophysiological response will be elicited. If two tones are separated by an interval longer than the critical temporal integration window, they will not be integrated and two electrophysiological responses will be elicited. Based on the asymmetric sampling in time hypothesis (Poeppl, 2003), it was predicted that when tones were separated by an inter-stimulus interval (ISI) of 50 ms, a second electrophysiological response would only be observed over the left hemisphere, as the tones would only be integrated by the long temporal integration window of the right auditory cortex. For the 200 ms ISI tone-pairs, it was predicted that a second electrophysiological response would be observed over both the left and right hemispheres, as the tones would not be integrated by either the short or the long temporal integration window.

2. Materials and method

2.1. Participants

Reliable auditory ERPs were available from twenty-seven participants (10 male; 24 right-handed,) aged between 18 and 23 years old ($M=19.93$ years, $SD=1.77$ years) following data screening procedures outlined by Fox et al., (2012). Participants were recruited from The University of Western Australia to take part in the study. All participants provided informed consent. The Human Research Ethics committee of The University of Western Australia approved the protocol for the study.

2.2. Auditory stimuli

The test stimuli were composed of standard 20 ms, 1000 Hz sinusoidal tones with 2 ms ramped onset and offset. Sound intensity was calibrated using a 1 s continuous 1000 Hz sinusoidal 72 dB SPL tone measured by a Brüel and Kjaer sound level meter. There were three stimulus types: a single tone stimulus, and two

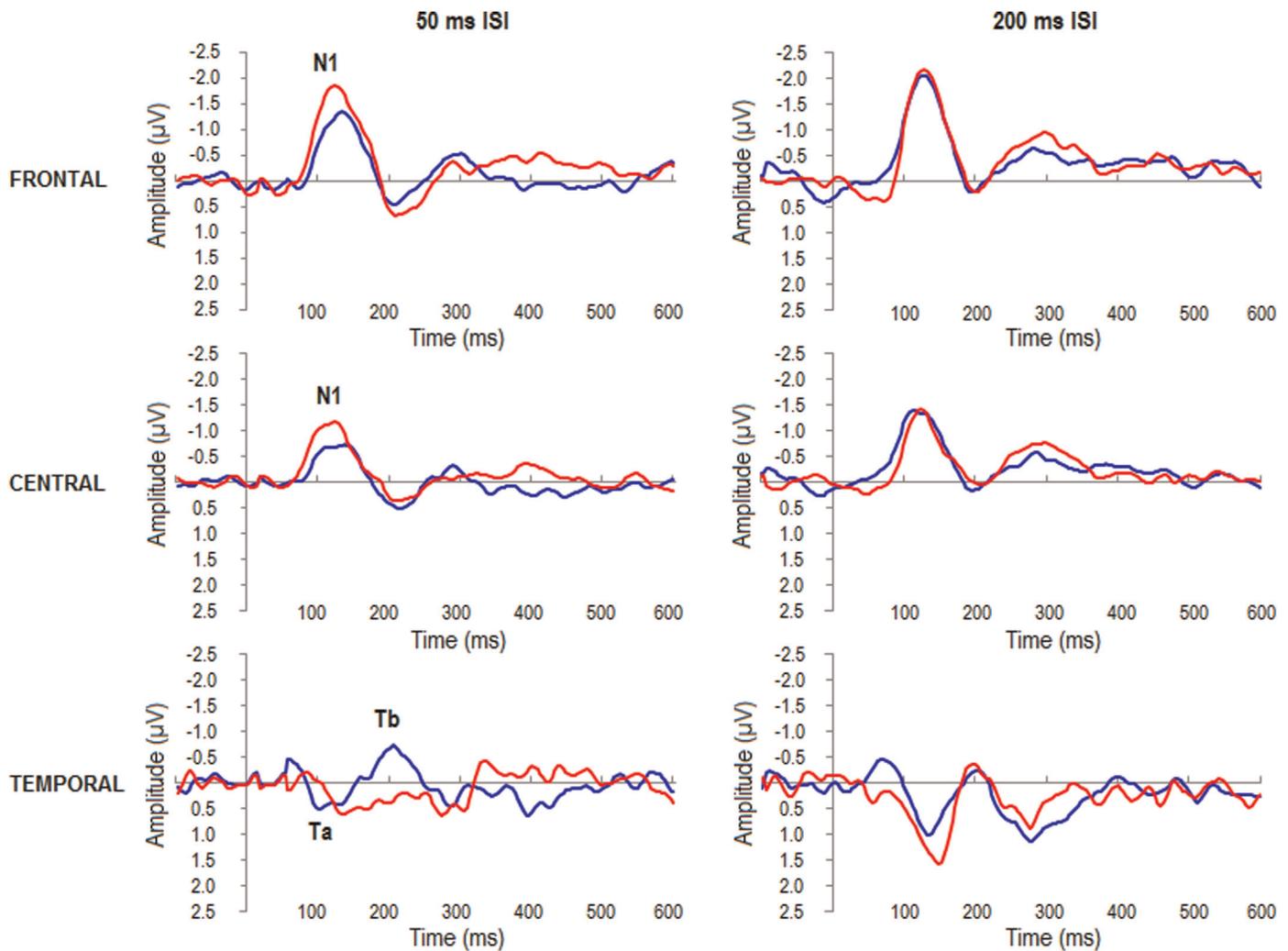


Fig. 2. Grand-averaged ERPs elicited in response to the second tone of the tone pairs presented at ISIs of 50 ms and 200 ms. The amplitudes of the waveforms measured over the left (blue/black) and right (red/grey) hemispheres at frontal, central, and temporal sites are given in microvolts (μV).

paired-tone stimuli, each composed of two standard tones that were separated by different ISIs (50, 200 ms). Each trial was set to 1500 ms in duration, where stimulus onset times were randomly jittered between 0–200 ms from the start of each trial. In addition, 600 ms ISI tone pairs were presented to determine whether a reliable auditory ERP was elicited (Fox et al., 2012).

2.3. Procedure

Participants were fitted with an EasyCap™ at the beginning of the testing session. Auditory stimuli were presented to participants binaurally via a set of Sennheiser HD 265 adjustable headphones placed over the ears. The task consisted of 400 trials, 100 trials for each stimulus type, and lasted for approximately 10 min. We chose a passive task in order to reduce the influence of attention to stimuli on ERP amplitudes (Lang et al., 1995; Mahajan and McArthur, 2013; McArthur et al., 2003; Naatanen, 1995). Participants were instructed to ignore the tones and were provided with reading materials (picture books with minimal text) and hand-held electronic games (audio switched off) to aid their distraction. If at any time the participant's activity was interfering with the EEG recording (e.g. excessive eye movements), they were instructed to change activities.

2.4. Data acquisition

Data were acquired and processed offline using SCAN™ 4. Electrophysiological activity was continuously recorded via electrodes located at 33 scalp locations (Fp1, Fp2, F3, F4, F7, F8, Fz, FC1, FC2, FC5, FC6, FCz, FT9, FT10, C3, C4, Cz, T7, T8, CP1, CP2, CP5, CP6, P3, P4, P7, P8, Pz, PO9, PO10, O1, O2, Iz). Channel impedances were limited to below $10\text{ k}\Omega$ prior to recording. Channels with impedances exceeding $10\text{ k}\Omega$ were excluded from further analyses. The EEG was amplified using a NuAmps 40-channel amplifier, digitised at a sampling rate of 250 Hz, and filtered online using a 0.01–30 Hz band-pass filter. AFz was set as the ground and the electrode located at the right mastoid was set as the reference. A common averaged reference was calculated offline. Vertical ocular artifacts were removed via a regression algorithm (Semlitsch et al., 1986) using the recordings from two ocular leads placed 2 cm above and below the left eye. The EEG was digitally filtered offline using a 1–30 Hz zero phase-shift band-pass filter (12 dB roll-off). Epochs were segmented from 100 ms pre-stimulus onset to 1000 ms post-stimulus onset. Averaged-waveforms were baseline corrected around the 100 ms pre-stimulus interval. Epochs that contained artifacts exceeding $\pm 150\text{ }\mu\text{V}$ were rejected. Following epoch rejection, the average numbers of epochs included per participant were 97.44 for the single tone, 97.19 for the 50 ms ISI tone pairs, 97.44 for the 200 ms ISI tone pairs, and 97.07 for the

600 ms ISI tone pairs.

2.5. Correction for response overlap

As we were interested in analysing the electrophysiological response to the second tone of each tone pair, we needed to correct for the overlap between the ERPs elicited by the first and second tone of each tone-pair. We subtracted individual-averaged single tone waveforms from individual-averaged paired-tone waveforms for each participant. The subtraction allowed us to isolate the response elicited by the second tone in each condition (Fox et al., 2010; Sable, Low et al., 2004). The waveforms were then stimulus-locked such that the onset of the second tone was set to time zero, allowing the waveforms to be compared across conditions. The resulting waveforms were then baseline corrected using the 100 ms pre-stimulus interval for the respective condition. The grand averaged waveforms synchronised to the onset of the first tone are presented in Fig. 1 and grand averaged waveforms elicited in response to the second tone of the tone-pairs are presented in Fig. 2, showing the left and right hemisphere waveforms superimposed. In the following sections, references to and discussions of data refer to the N1 and T-complex responses to the second-tone of each tone pair (with the exception of Section 3.4 reporting a supplementary analysis investigating the potential impact of signal-to-noise level on the obtained results).

2.6. Topographic distribution of ERPs

The N1 and the T-complex were extracted from sites where the amplitude was largest. The topographic distribution of the neural response to the single tone and response overlap corrected paired-tone conditions indicated that the N1 was largest at fronto-central sites (Fz, F3, F4, Cz, C3, and C4), and the T-complex was largest at temporal (T7 and T8) sites. To allow for the comparison of responses between hemispheres, ERPs were extracted from electrode pairs F3/F4 and C3/C4 for the N1, and T7/T8 for the T-complex.

2.7. Extraction of mean amplitudes

Different latency windows were calculated for each ISI to take into account latency differences between conditions. Based on the grand-averaged waveforms for each ISI, the peak latency of the peak was measured at each site, and averaged together to calculate the average peak latency for the relevant peak in the respective ISI. Mean amplitudes were calculated based on an interval two points (8 ms) either side of the average peak (20 ms window) for each peak and ISI (Hakvoort et al., 2014). The latency intervals over which each of the mean amplitudes were calculated were 120–136 ms (N1 50 ms ISI), 116–132 ms (N1 200 ms ISI), 108–124 ms (Ta 50 ms ISI), 132–148 ms (Ta 200 ms ISI), 200–216 ms (Tb 50 ms ISI), and 188–204 ms (Tb 200 ms ISI).

2.8. Data analysis

All data were subject to preliminary screening measures prior to statistical analyses to ensure that all the assumptions of ANOVA were met. Skew and kurtosis coefficients were used to assess the normality of the data. Skew and kurtosis coefficients were divided by the respective standard error and the computed values were compared to a critical value of ± 3.29 as outlined by Tabachnick and Fidell (2001). Data were winsorized to reduce the effect of spurious outliers as outlined by Wilcox (2001). Three repeated-measures ANOVAs were conducted. The N1 mean amplitudes were subject to a $2 \times 2 \times 2$ repeated-measures ANOVA, with site (frontal, central), hemisphere (left, right), and ISI (50 ms, 200 ms) as the

within-subject variables. Ta and Tb mean amplitudes were subject to separate 2×2 repeated-measures ANOVAs, with hemisphere (left, right) and ISI (50 ms, 200 ms) as the within-subject variables.

3. Results

Descriptive statistics of all extracted ERP components are presented in Table 1.

3.1. Analysis of the mean N1 amplitudes of the response corrected waveforms

The N1 mean amplitudes were larger over frontal sites than over central sites ($F(1, 26)=36.73$, $p < 0.001$, $\eta_p^2=0.586$), and for the 200 ms ISI than the 50 ms ISI ($F(1, 26)=13.23$, $p < 0.01$, $\eta_p^2=0.337$), however, there was no difference in N1 mean amplitudes across hemispheres ($F(1, 26)=2.52$, $p=0.124$, $\eta_p^2=0.088$). The interaction between ISI and hemisphere approached significance ($F(1, 26)=3.56$, $p=0.071$, $\eta_p^2=0.120$), but the interactions between site and hemisphere ($F(1, 26)=0.81$, $p=0.376$, $\eta_p^2=0.030$), site and ISI ($F(1, 26)=0.12$, $p=0.730$, $\eta_p^2=0.005$), and site, hemisphere and ISI ($F(1, 26)=0.01$, $p=0.906$, $\eta_p^2=0.001$) were not significant.

3.2. Analysis of the Ta mean amplitudes of the response corrected waveforms

The Ta mean amplitudes were larger for the 200 ms ISI than the 50 ms ISI ($F(1, 26)=28.31$, $p < 0.001$, $\eta_p^2=0.521$). There was no significant difference in Ta mean amplitudes across hemispheres ($F(1, 26)=0.73$, $p=0.401$, $\eta_p^2=0.027$), nor was the interaction between hemisphere and ISI significant ($F(1, 26)=2.66$, $p=0.115$, $\eta_p^2=0.093$).

3.3. Analysis of the Tb mean amplitudes of the response corrected waveforms

There was no significant effect of hemisphere ($F(1, 26)=2.23$, $p=0.147$, $\eta_p^2=0.079$) or ISI ($F(1, 26)=0.27$, $p=0.607$, $\eta_p^2=0.010$). A significant interaction between hemisphere and ISI was identified ($F(1, 26)=4.45$, $p=0.045$, $\eta_p^2=0.146$), and was followed up with post-hoc pairwise comparisons of the left and right hemispheres for each condition. The Tb mean amplitudes were significantly smaller over the right hemisphere than over the left hemisphere when tones were presented 50 ms apart ($t(26)=-2.32$, $p=0.028$, $d=0.45$), but were similar when tones were presented 200 ms

Table 1

Descriptive statistics of the mean amplitudes (μV) of the N1, Ta and Tb for each ISI, at each site.

| Site | ISI | |
|------|---------------|---------------|
| | 50 ms | 200 ms |
| | (M, SD) | (M, SD) |
| N1 | | |
| F3 | - 1.27 (0.86) | - 2.01 (1.05) |
| F4 | - 1.80 (1.17) | - 2.11 (1.06) |
| C3 | - 0.70 (0.66) | - 1.35 (0.95) |
| C4 | - 1.10 (0.70) | - 1.35 (0.84) |
| Ta | | |
| T7 | 0.41 (1.14) | 0.93 (1.26) |
| T8 | 0.29 (1.20) | 1.49 (1.18) |
| Tb | | |
| T7 | - 0.63 (1.25) | - 0.18 (0.97) |
| T8 | 0.30 (1.24) | - 0.32 (0.94) |

apart ($t(26)=0.44$, $p=0.665$, $d=0.08$).

3.4. Analysis of signal-to-noise level

To check that the smaller amplitude of the Tb peak over the right hemisphere in the 50 ms condition was not due to increased noise of the ERPs, the intraclass correlation coefficient (ICC) between the single and paired-tone responses (50 and 200 ms) were calculated for the first 100 ms of the waveform (i.e. prior to the onset of the second tone during which time ERP responses should not differ). If the above critical interaction between hemisphere and ISI were simply due to increased noise, we would expect the analysis of ICCs to follow the same pattern. There was no significant interaction between hemisphere and ISI ($F(1, 26)=0.88$, $p=0.357$, $\eta_p^2=0.033$).

4. Discussion

The objective of the present study was to investigate whether the left and right auditory areas integrate auditory signals according to temporal integration windows of different durations. It was hypothesised that an electrophysiological response (observed as a deflection in the ERP) would be elicited by the second tone of the 50 ms tone-pair over the left hemisphere but not over the right, as the right auditory areas would integrate the second tone with the first. It was also predicted that a response would be elicited by the second tone of the 200 ms ISI tone-pairs over both hemispheres as auditory areas in neither hemisphere would integrate the second tone with the first.

4.1. Evidence in support of the asymmetric sampling in time hypothesis

Poeppel (2003) proposed that auditory signals are initially processed symmetrically according to similar temporal integration windows in the primary auditory cortices, and are then elaborated asymmetrically according to different temporal integration windows in the secondary auditory cortices. We demonstrated support for the asymmetric sampling in time hypothesis in two ways: we provide evidence for the symmetric temporal integration of auditory signals for components that have been source localised to the primary auditory cortex, and we provide evidence for asymmetric temporal integration of auditory signals for components that have been source localised to the secondary auditory cortex. We also observed that the asymmetries were reflected in the later Tb peak rather than the earlier N1/Ta peaks suggesting the asymmetry could be associated with higher-level auditory processes such as speech processing.

4.1.1. Hemispheric symmetries in temporal integration

Temporal processing according to symmetrical short temporal integration windows was observed for the N1 and Ta components. Both N1 and Ta responses were elicited by the second tone in the 50 ms condition, suggesting that the neural generators of the N1 and Ta function according to a short temporal integration window of < 50 ms. As the N1 and Ta have been source localised to the primary auditory cortex (Bishop et al., 2011), our findings support the conjecture that auditory signals are processed symmetrically according to a short temporal integration window in primary auditory areas (Poeppel, 2003). The short temporal integration window is proposed to correspond to the gamma frequency band (~20–40 Hz), based on this supposition our findings are consistent with previous reports of bilateral gamma frequency activity (Luo and Poeppel, 2012) and the observation of bilateral activation of primary auditory areas in response to increased temporal

variation (Jamison et al., 2006).

4.1.2. Hemispheric asymmetries in temporal integration

Temporal processing according to asymmetric temporal integration windows was observed for the Tb component. Over the right hemisphere a second Tb response was elicited when tones were separated by a 200 ms ISI, but not when tones were separated by a 50 ms ISI suggesting that the second tone was integrated with the first in the latter ISI. These results suggest that the areas from which the Tb originates in the left hemisphere operate according to a short temporal integration window (≤ 50 ms), and the areas from which the Tb originates in the right hemisphere operate according to a longer temporal integration window that is longer than 50 ms but less than 200 ms. This finding is consistent with the asymmetric sampling in time hypothesis (Poeppel, 2003).

The long temporal integration window observed over the right hemisphere is proposed to correspond to the rightward lateralisation of theta band responses, and the short ~50 ms window observed over the left hemisphere corresponds to the leftward lateralisation of gamma band responses reported in previous studies (Boemio et al., 2005; Giraud et al., 2007; Luo and Poeppel, 2012). Furthermore, the Tb has been shown to originate from the secondary auditory cortices, which is consistent with the source of the lateralised activity associated with the processing of slow modulations (Boemio et al., 2005). Secondary auditory areas are associated with higher-order processes, further supporting the association between the asymmetries in temporal integration processes and their potential purpose for higher-level auditory processes.

4.1.3. Advances from previous research on hemispheric asymmetries in temporal integration

Our findings demonstrate how auditory signals are integrated in high-order auditory areas according to temporal features. The asymmetries in temporal integration windows may account for observed differences in the involvement and temporal resolving power of the left and right hemispheres in auditory processing tasks and could explain why patients with right hemisphere damage can still complete temporal processing tasks. Data from behavioural studies of patients who acquired unilateral lesions to the posterior temporal and inferior parietal regions of the left hemisphere show that temporal processing abilities are poorer but are not completely lost (Divenyi and Robinson, 1989; Robin et al., 1990). Such patients require longer intervals between successive stimuli to discriminate them when compared to control individuals, suggesting that the left hemisphere plays an important role in the processing of rapidly presented auditory signals (Divenyi and Robinson, 1989; Robin et al., 1990). It has been suggested that the persistence of temporal processing capabilities is due to the preservation of areas in the right hemisphere that are homologous to those involved in rapid temporal processing.

Importantly, our findings show that asymmetries in temporal integration processes are characteristic of particular auditory areas. Specifically, hemispheric asymmetries were observed for the component associated with secondary auditory areas, but not in those associated with primary areas. Being able to differentiate between sources of activity within each hemisphere was crucial to our ability to observe both symmetries and asymmetries in temporal integration processes. Luo and Poeppel (2012) investigated the lateralisation of theta and gamma band phase coherence using MEG. They compared the grand-averaged phase coherence values of the left hemisphere with those of the right hemisphere, for both frequency bands. They observed the lateralisation of theta band activity to the right hemisphere, but found no lateralisation of gamma band activity. According to the asymmetric sampling in

time hypothesis, gamma band activity is observed bilaterally in the primary auditory cortices but is lateralised to the left hemisphere in the secondary auditory cortices. We suggest that their analyses may not have been sensitive to the lateralisation of gamma band activity as they compared overall hemispheric activity, rather than the activity of specific channels within each hemisphere as was done in the current study. Therefore, the absence of hemispheric asymmetries in gamma band activity may have been masked by clustering together channels reflecting activity of both primary and secondary auditory areas. By looking at components that reflect the activity of primary and secondary auditory areas separately, we were able to provide evidence for asymmetries as well as asymmetries in temporal integration processes.

4.2. Limitations and directions for future research

4.2.1. Signal-to-noise issues

In the present study, we examined the N1 and T-complex components of auditory ERPs. The fronto-central N1 is a large ERP component that is generally observable in adults. On the other hand the Ta and Tb reduce in amplitude from childhood to adulthood, becoming less distinguishable and more susceptible to noise in adults (Tonquist-Uhlen et al., 2003). As such, the issue of noisy ERPs is problematic for the analysis of these components in adults. To address this issue we used a common-averaged reference and carried out an analysis of noise using the ICC to rule out the possibility that the observed pattern of results was due to increased noise.

The type of reference used when analysing temporal ERP components can have a great impact on the noisiness of the observed waveforms. Although many studies use a linked-mastoid reference for ERP analyses, a linked-mastoid reference can diminish the T-complex response given the close proximity of the mastoid reference sites to the lateral temporal sites where the Ta and Tb are maximal. Therefore, to increase the signal-to-noise ratio we recommend that researchers use a common-averaged reference as was used in the present study.

In order to confirm that the observed pattern of results was not due to noisier ERPs over the right hemisphere for the 50 ms condition, ICCs between the single and paired-tone responses (50 and 200 ms) were calculated for the first 100 ms of the waveforms. If a particular hemisphere or ISI were noisier than the other, the ICCs for that hemisphere or ISI would be significantly lower in comparison. Importantly, we found no significant interaction between hemisphere and ISI, suggesting that the noisiness of waveforms did not vary depending on the combination of hemisphere and ISI. As such, we are confident that the observed difference in amplitude observed in the 50 ms ISI condition between the left and right hemisphere was not due to noisier waveforms. Moreover, auditory ERPs elicited by tone stimuli similar to those used in the current study are typically reported to be larger over the right hemisphere than over the left hemisphere (Wolpaw and Penry, 1977), therefore if noise were to affect the data, one would expect to observe the attenuation of ERPs over the left hemisphere, rather than over the right hemisphere.

4.2.2. Estimation of temporal integration windows

In the current study we used two key ISIs that we believed best reflected the hypothesised temporal integration windows associated with each hemisphere (50 and 200 ms). In doing so, we were able to demonstrate differences in the temporal integration windows of each hemisphere with areas of the left hemisphere being associated with short temporal integration window of less than 50 ms, and areas of the right hemisphere being associated with a longer temporal integration window between 50 and 200 ms in duration. As we did not use any extremely short or

intermediate ISIs, we were only able to provide a rough estimate (i.e. short - less than 50 ms and long - between 50 and 200 ms) for each temporal integration window. Future studies should include shorter ISIs of 10 and 25 ms to provide a better estimate of the short temporal integration window as well as intermediate ISIs such as 100 and 150 ms to allow for a narrower range for the estimate of the long temporal integration windows.

4.2.3. Cerebral lateralisation of language

An important conjecture relating to the asymmetric sampling in time hypothesis is that the proposed pattern of temporal integration is relevant for individuals with typical leftward lateralisation of language. Unfortunately, we did not have confirmation of hemispheric dominance for language in each participant. As handedness has been shown to be a poor proxy for cerebral lateralisation of language (Groen et al., 2011), we chose not to exclude left-handed participants. Including individuals who were rightward-lateralised for language would have reduced the power of the study. Although this issue did not affect the power to detect the effect of interest in the present results, it may have masked other smaller effects present in the sample. Future studies should attempt to include some measure of cerebral lateralisation of language to investigate whether the hemisphere that is dominant for language is also associated with the short temporal integration window.

In addition to the aforementioned recommendations, we believe that future studies should attempt to examine the asymmetric sampling in time hypothesis in children, in order to understand the development of lateralised temporal processes. This is particularly important as poor lateralization of auditory processing may be linked to the development of poor language abilities (Bishop et al., 2012; Goswami, 2011; Johnson et al., 2013; Shafer et al., 2011).

5. Conclusion

Our findings reveal that there is both symmetric and asymmetric integration of auditory signals occurring within the left and right auditory areas of adults. We have demonstrated that the ERP components that originate from auditory areas where temporal integration is symmetric and auditory areas where temporal integration is asymmetric are dissociable using a simple paired-tone paradigm. Key to our findings was the observation that asymmetries in the temporal integration of auditory stimuli only occur in auditory areas that generate the Tb component.

We therefore propose that the Tb is an important component of the auditory ERP, and should be further investigated to understand the cognitive processes that may be associated with the Tb response. Following from Poeppel's (2003) theory of a multi-time resolution model of auditory processing, we propose that the Tb response could index the segmentation of the continuous auditory signal into meaningful units relevant for higher-level auditory processing, as suggested in the asymmetric sampling in time hypothesis.

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