



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



Karen L. Clunies-Ross^{a,*}, Christopher R. Brydges^{a,b}, An T. Nguyen^a, Allison M. Fox^a

^a Neurocognitive Development Unit, School of Psychology, The University of Western Australia, M304, 35 Stirling Highway, Crawley, Western Australia 6009, Australia

^b School of Psychology and Exercise Science, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia

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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 (Poehppel, 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 (Poehppel, 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. Poehppel (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 (Poehppel, 2003; Poehppel et al., 2008). Poehppel (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). Poehppel (2003) proposed that the purpose of the short temporal integration window was for the processing of rapid modulations such as phonetic transitions (Poehppel, 2003; Poehppel et al., 1996), and the

* Corresponding author.

E-mail address: Karen.clunies.ross@graduate.uwa.edu.au (K.L. Clunies-Ross).

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

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