International Congress Series 1300 (2007) 29 – 32

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Phase dynamics in the 40-Hz auditory steady state response

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Abstract. The phase of the 40-Hz auditory steady-state response (SSR) evoked by amplitude-modulated tones and recorded by MEG decreases monotonically with increasing carrier frequency, shifting about 6.25 ms or 90° over the range 250–4000 Hz. This phase shift has been attributed to propagation delays along the basilar membrane. Here we report that the slope of the SSR phase/carrier frequency characteristic is not invariant but depends on contextual factors relating to stimulus presentation. When steady-state stimuli were presented continuously with a random change to one of four carriers occurring every second, the phase difference between 500 and 1000 Hz was amplified by a factor of 2.5 compared to when the same frequencies were presented without shifting (baseline). Changing carrier frequencies in a predictable fixed order once per second resulted in a phase separation 1.6 times larger than baseline. We also tested whether a carrier frequency change was required to generate this wider phase separation. We presented continuous 15 min blocks at constant carrier frequencies of 500 or 1000 Hz, interrupted regularly once per second by increasing the amplitude of one modulation cycle. Once about every three seconds the enhancement occurred in only one ear, yielding a distinctive percept (target). The phase difference between 500 and 1000 Hz increased by 1.54 compared to baseline, regardless of whether the subject was attending to the target. Taken together, these results suggest that any disturbance in an on-going steady stimulus is sufficient to change the phase of the SSR for a period of time lasting on the order of several seconds or longer. The mechanisms responsible are unknown although a contribution of cortical dynamics to SSR phase is implied. © 2007 Elsevier B.V. All rights reserved.

Keywords: Evoked potential; Auditory cortical plasticity; 40 Hz auditory steady-state response

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0531-5131/
doi:10.1016/j.ics.2006.12.099

1. Introduction

Auditory cortical neurons alter their membrane dynamics as the rate of acoustic stimulation increases [1]. At rates above about 3 Hz temporal integration by EPSPs becomes selective for short latency inputs which may underlie AEPs and AEFs evoked by repetitive stimulation. An example is the auditory "steady state response" (SSR) which is maximal when evoked by carrier frequencies amplitude modulated (AM) at rates near 40 Hz. The summation of auditory "middle latency responses" (MLRs, these usually recorded at rates above 3 Hz) appears to explain the SSR waveform over a range of AM rates, including its amplitude maximum near 40-Hz [2,3] although stabilized networks underlying the MLR waveform may be sculpted by nonlinear interactions.

Investigations of the 40-Hz SSR have found that as the carrier frequency of the AM stimulus increases, SSR phase decreases [4]. This effect has been attributed to the travelling time of waves on the basilar membrane [5,6]. Here we show that the relation of phase to carrier frequency is not fixed but varies substantially with task conditions, implying that factors in addition to travelling delays determine SSR phase.

2. Methods

40 students at McMaster University aged 17–30 years (Mean = 20, 16 male) with normal hearing provided written consent. Carrier frequencies of 500, 650, 800 and 1000 Hz were amplitude modulated at 40 Hz. All stimuli were presented binaurally at 60dB SPL via Etymotic ER2 ear inserts. Except where indicated, subjects watched a subtitled silent movie. Procedures differed as described below for three separate experiments.

128 channel EEG (Biosemi ActiveTwo) was sampled at 512 Hz (low pass-3dB at 100 Hz, reference at Cp1 and ground at Cp2 10-10). EEG responses were epoched into 1 s segments with 200 ms pre/post baselines, filtered 39–41 Hz, and averaged after selecting approximately 90% artifact-free segments. A 64-point hamming window was moved across the average and the 40 Hz component of the FFT of this window calculated for each time point giving SSR amplitude and phase. Phase was corrected to portray the phase difference between the stimulus and the response at each time point.

3. Experiment 1 — blocked vs. random condition

Two stimulus conditions were used in this experiment. In the Blocked condition, 15 min of each carrier frequency (500, 650, 800, and 1000 Hz) were presented continuously in an ascending or descending order. In the Random condition, the carrier frequency changed randomly among the four frequencies once each second, with the same total amount of stimulation at each carrier (15 min) as in the Blocked condition.

The results are shown in Fig. 1. In the Blocked condition (Fig. 1A), there was a 20 degree phase separation between 500 Hz and 1000 Hz, which is in agreement with published data relating phase to carrier frequency collected under similar conditions [4] and arguably within the range of travelling delays estimated for these frequencies [6]. Fig. 1B shows that after an initial transient response, the phase separation between 500 and 1000 Hz increased from 20° to 50° (250%) when carrier frequency changed every second in a

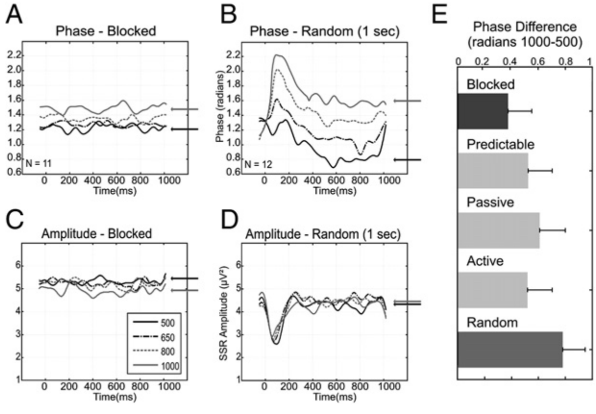

Fig. 1. SSR phase for four carrier frequencies each presented in 15 min blocks (A) or changing randomly once/per second for 60 min (B). SSR amplitude is shown in (C) and (D). Panel (E) shows the phase difference between 500 and 1000 Hz for all experimental conditions (see text for details).

random order. The difference in phase separation between Blocked and Random was statistically significant ($p<0.02$).

Fig. 1C and D present the corresponding amplitude data. In the blocked condition there was a shallow but discernable inverse relationship between SSR amplitude and carrier frequency which is again consistent in magnitude with published data for blocked arrangements [4]. In the random condition, SSR amplitude stabilized at slightly lower values after an initial perturbation, and the relationship of amplitude to carrier frequency appeared to be blurred.

4. Experiment 2 — fixed presentation order

Subjects ($n=11$) experienced 40-Hz AM carrier frequencies of 500, 650, 800, and 1000 Hz changing every second as in the Random condition of Experiment 1. However, the stimuli were presented in a predictable ascending order. With this procedure there was a clear ordering of phase in relation to carrier frequency, corresponding to previous data. However, the phase separation between 500 and 1000 Hz was intermediate between that of the blocked and random groups of Experiment 1 (1.6× the former), and statistically smaller ($p=0.04$) than in the random group (Fig. 1E). SSR amplitude was similar to that observed in Fig. 1D, with no discernable relation to carrier frequency.

5. Experiment 3 — attention

Subjects ($N=9$) were presented with 500 and 1000 Hz carrier frequencies separately, AM at 40 Hz. The tones were played continuously to the subjects binaurally. For every 40th pulse, pulse amplitude was increased to 250% of normal producing a regular metronome-like signal with a period of 1 s. At random intervals in this sequence, the increased-amplitude pulse to one ear (chosen randomly) was reduced to 101% of normal, which produced a subjective shift in the tone towards the other ear. The shift occurred about once every three seconds. In passive blocks of 5 min duration, subjects watched a silent video. In active blocks of the same duration (attention condition — video discontinued), subjects pressed a button to signal which ear the tone shifted towards.

The phase response followed a course similar to 500 and 1000 Hz in the random condition of Experiment 1. However, the phase separation between 500 and 1000 Hz was intermediate between the random and blocked groups of Experiment 1 (mean 1.54 × blocked) with no difference between the passive and attend conditions (Fig. 1E).

6. Discussion

The results suggest that SSR phase depends on more than delays attributable to the travelling wave on the basilar membrane. Such delays presumably determine phase ordering with respect to carrier frequency, but additional variables contribute [6].

The phase segregation effect seen in Fig. 1A,B implies that the specific population of neurons representing each carrier frequency changed when the stimulus procedure was modified. However, the amplitude data suggest that the size of the representation (number of neurons recruited by the AM envelope) did not change substantially although the relationship of amplitude to carrier frequency may have been abolished. We suggest that competitive interactions within the region of A1 may normalize the number of neurons representing different carrier frequencies when perturbations are present in the stimulus procedure. Under these conditions carrier frequency may be represented not only by cortical place maps but also by sub-populations of neurons that are segregated on the basis of temporal response properties.

Our exploration of predictability and attention produced intermediate effects on phase compared to the endpoints of blocked and random. Although we have not yet identified the critical factor(s) that determine the effect, the experiments spanned a significant portion of the parameter space. Stimulus procedures that evoke transient auditory responses (P1/N1/P2, not shown here) may result in phase segregation which outlasts the transient period, although segregation must eventually subside.

Acknowledgement

Supported by CHR and NSERC of Canada.

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