

Generation of human auditory steady-state responses (SSRs). I: Stimulus rate effects

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Abstract

Auditory evoked responses were recorded in 16 normally hearing subjects in order to investigate the mechanisms underlying the generation of the 40 Hz steady-state response (SSR). In the first part of our study, auditory potentials were evoked by 0.1 ms clicks presented at 105 dB p.e. SPL with repetition rates of 7.9 (to obtain middle latency response, MLR), 20, 30, 40, 50, 60 Hz.

In each subject predictions of the responses recorded at stimulus repetition rates of 30, 40, 50, 60 Hz were synthesized by superimposing MLRs at suitable time intervals. The calculated mean amplitude/rate and phase/rate functions behaved similarly for the recorded and predicted curves, showing the highest amplitude at 40 Hz and a linear increase of phase values when increasing the stimulus rate. Nevertheless the synthetic curves closely predicted amplitude and phase values of the recorded responses only at 40 Hz. At frequencies below 40 Hz, the mean amplitude of the predicted curve was lower than that of the recorded one while at frequencies above 40 Hz the mean amplitude was higher. Predicted phase values were found lagging at 30 Hz, and leading at 50 Hz and 60 Hz in comparison to phase values calculated on the recorded responses.

Our findings suggest that a model based on the linear addition of transient MLRs is not able to adequately predict steady-state responses at stimulus rates other than at 40 Hz. Other mechanisms related to the recovery cycle of the activated system come into play in the steady-state response generation causing a decrease in amplitude and an increase in phase lag when increasing the stimulus repetition rate.

Keywords: Middle latency response; Steady-state response; Repetition rate; Adaptation; Auditory system

1. Introduction

The auditory 40 Hz steady-state response (SSR) was first recorded by Galambos and co-workers (1981) in human beings by utilizing clicks or tone bursts at a rate of 40 Hz. This response resembles a 40 Hz sine-wave and it has a consistent amplitude at intensities close to the behavioural threshold, and increasing amplitudes with a lowering of the tone frequency in burst stimulation (Galambos et al., 1981; Stapells et al., 1984). Due to these features, the 40 Hz-SSR seemed to be a promising diagnostic tool in detecting hearing impairment in the low frequency range (Galambos et al., 1981; Stapells et al., 1984; Sturzebecher et al., 1985;

Lenarz et al., 1986). Nevertheless the optimal use of the 40 Hz-SSR in diagnostics requires knowledge of the mechanisms underlying its generation. At present there is no general agreement with respect to this problem. However two main hypotheses have been advanced.

The first hypothesis assumes that the auditory neural network displays an intrinsic rhythm that would be more or less well-driven depending upon the stimulus rate (Galambos, 1982; Basar et al., 1987). This assumption is supported by the results of several studies. First of all, the auditory as well as other sensory systems show several spontaneous and event-related activities in the so-called gamma-band (Galambos and Makeig, 1988; Bressler, 1990) and these activities represent possible basic physiological mechanisms underlying perceptive processes (Barinaga, 1990; Crick and Koch,

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1990; Pantev et al., 1991; Tiitinen et al., 1993). Moreover, an activity around 40 Hz has been shown in direct recordings from several brain sites in response to different sensory stimulations (Basar et al., 1979a; Basar et al., 1979b; Basar, 1980; Bressler and Freeman, 1980; Bouyer et al., 1981). Finally, the 40 Hz spontaneous EEG activity has been demonstrated to determine the parameters of the middle latency response (MLR) (Basar et al., 1987). According to this hypothesis, the system behaves as a tuned oscillator in the presence of a suitable periodic input and both the steady-state 40 Hz response and the transient middle latency response could be regarded as the output of this oscillator in different states of activation. Thus, the 40 Hz enhancement may be considered to reflect a more general property of the brain network, behaving as a neural resonator tuned to a frequency of 40 Hz.

The second hypothesis, which was first suggested by Galambos and his colleagues (1981), states that the 40 Hz-SSR results from the linear addition of MLRs evoked by individual clicks during steady-state stimulation, since the time interval between MLR peaks of the same polarity results very close to the 40 Hz-SSR period. This view is supported by the close correspondence between the recorded 40 Hz-SSR and the 40 Hz prediction curve obtained by superimposing individual MLRs shifted by suitable intervals. The effectiveness of this model has been verified in animals (Ottaviani et al., 1990) as well as in human beings (Galambos et al., 1981; Stapells et al., 1988; Hari et al., 1989; Plourde et al., 1991) by electric and magnetic recordings. Furthermore, this hypothesis is supported by the evidence of a common cortical generator of both the MLR and the 40 Hz-SSR in humans (Mäkelä and Hari, 1987; Hari et al., 1989; Pantev et al., 1993).

These reported findings and conclusions deserve some comment.

Firstly, the resemblance of the predicted curve to the recorded one is a necessary but not sufficient condition to rule out a resonance phenomenon. In fact, one can obtain a good fitting of the 40 Hz-SSR by utilizing various exponentially damped harmonic oscillations with convenient values of angular frequency, modulus and damping ratio as the basic response. Moreover, a distinction should be made between linearity and stability. In fact, a system having an intrinsic rhythm is not stable due to the presence of an output in absence of an input. However, a system having a resonant frequency may be stable and linear. In this view, the question whether the genesis of the 40 Hz-SSR should be attributed to a linear summation of individual responses or to a resonance phenomenon appears misleading because the two hypotheses are not mutually exclusive.

There is also another point to be considered. Stapells et al. (1984) have suggested that some non-linearities

related to the relative refractory period could influence the generation of the steady-state response. In fact, amplitude and latency changes of MLR components with increasing stimulus rates have been reported by several authors (Erwin and Buchwald, 1986; Kraus et al., 1988; Chambers, 1992; Picton et al., 1992). Hence, it would not be unreasonable to expect that the responses to individual clicks during steady-state stimulation be in some way different from the MLRs obtained at low repetition rates.

The above reported considerations suggest that the generation of the SSR is the result of a complex interaction of several mechanisms. Our research was aimed at highlighting the role played by other mechanisms besides the simple linear MLR addition to generate the auditory steady-state responses. In the present study, we addressed this issue: if the system generating the steady-state responses behaves in a linear fashion so that the 40 Hz-SSR results from the linear addition of the transient surface-recorded MLRs, we would expect to find a correspondence between the predicted curve and the recorded one not only at 40 Hz but also at other repetition rates. To this aim we compared the steady-state responses recorded at several stimulation rates with the SSR predictions synthesized by linear addition of individual MLRs shifted by suitable intervals.

The role eventually played by the system resonant properties will be considered in the following companion paper.

2. Material and methods

2.1. Subjects and stimulation paradigm

Sixteen healthy subjects (11 males, 5 females; aged 20–38 years) were studied. Informed consent was obtained from all subjects. None had a history of neurological or otological diseases. All had normal hearing with threshold within 15 dB HL at octave frequencies from 0.25 to 4 kHz (ISO 389, 1985). The subjects were tested while lying on a bed in a sound attenuated chamber. They were instructed to relax with their eyes closed and not to fall asleep, and the state of alertness was verified throughout the recording session.

Stimuli were given monoaurally by a TDH-49 earphone. They consisted in 0.1 ms clicks with alternating polarity presented at an intensity of 105 dB p.e. SPL (sound level meter Brüel and Kjaer 2231, artificial ear Brüel and Kjaer 4152) corresponding to 80 dB nHL in reference to the psychoacoustical threshold of normal hearing subjects.

Stimuli were presented at rates of 7.9, 20, 30, 40, 50, 60 Hz in a random order.

2.2. Recording

Electroencephalographic activity was recorded ipsilaterally to the stimulated ear using silver-chloride cup electrodes attached to the scalp with saline gel. The active electrode was applied to the vertex (Cz), the reference electrode was placed on the right or left mastoids (M1 or M2) and the ground electrode was placed on the forehead. Inter-electrode impedance was kept below 5 kOhms.

Signals were amplified (100 000) and filtered (5–3 000 Hz, 12 db/octave). Analogue to digital conversion was performed at a sample rate of 5 kHz (evoked potentials recording equipment EAC Mercury MDP 11/23 plus). Artefact rejection was active in order to avoid the recording of movement artefacts.

Two thousands epochs were averaged for each stimulus rate. At 7.9 Hz the waveform was replicated once in all the tested subjects. The time analysis window was 125 ms.

2.3. Data analysis

Individual MLRs were obtained by averaging the two replicated waveforms recorded at 7.9 Hz of repetition rate.

In each subject, prediction curves at 30, 40, 50 and 60 Hz were obtained by the linear addition of MLR traces shifted by suitable time intervals (33.4, 25, 20 and 16.6 ms at 30, 40, 50 and 60 Hz, respectively). To obtain the synthetic 40 Hz response, the 625 point-MLR curve was divided into five consecutive 125 point-segments, each corresponding to 25 ms. Then five consecutive 625 point-curves were summed in such a way that each curve was shifted by 25 ms with respect to the previous one (Fig. 1). A similar process was performed to obtain the synthetic 30, 50 and 60 Hz-responses. To synthesize the 30 Hz predicted response, the 625 point-waveform was cut to obtain a 501 point curve. This curve was divided into three consecutive 167 point-segments, each corresponding to 33.4 ms. Then three consecutive 501 point-waveforms were added in such a way that each curve was shifted by 33.4 ms with respect to the previous one. To synthesize the predicted curve of the 50 Hz response, the 625 point-curve was then divided into six 100 point-segments, each corresponding to 20 ms. Six consecutive 600 point-curves were added so that each curve was shifted by 20 ms with respect to the previous one. To obtain the prediction curve of the 60 Hz response, a 581 point-curve was obtained from the 625 point-curve by cutting the tail. The 581 point-curve was divided into seven 83 point-segments, each corresponding to 16.6 ms. Then, seven consecutive 581 point-curves were added in such a way

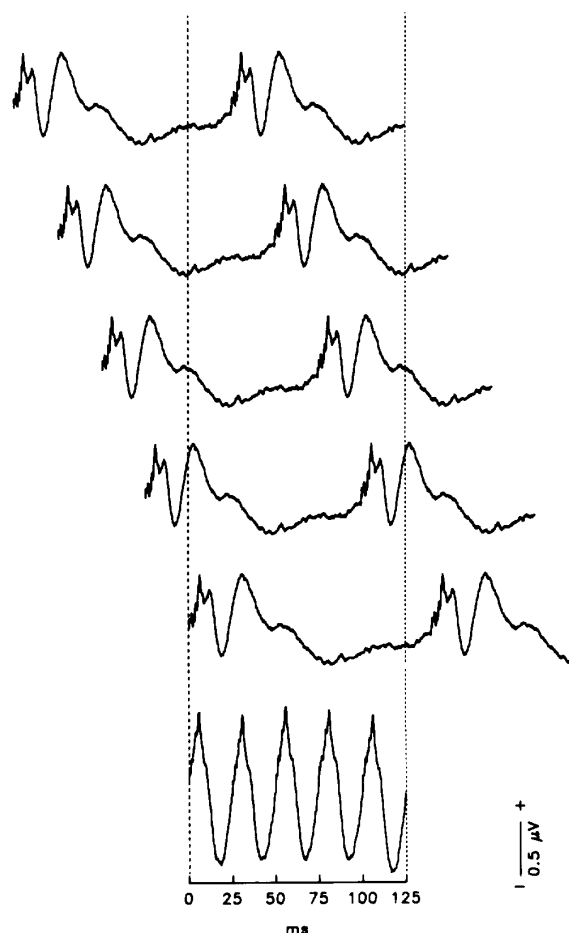


Fig. 1. Prediction of steady-state responses. The synthetic steady-state response (SSR) (bottom) was obtained by adding individual middle latency responses (MLRs) shifted by suitable time intervals. The example in the figure refers to synthetic 40 Hz-SSR obtained from the grand average of MLRs. Upward deflection indicates vertex positivity in this figure and in the subsequent ones.

that each curve was shifted by 16.6 ms with respect to the previous one.

The Fourier series technique was then applied to the recorded and synthesized curves to evaluate amplitude and phase values of the fundamental frequency. The recorded responses were suitably cut prior to submitting them to Fourier analysis in order to then obtain waveforms made up of an integer number of cycles at each repetition rate. Thus, the responses recorded at 20, 30, 50 and 60 Hz were cut at 500, 501, 600 and 581 points respectively, thus obtaining periodic curves showing two periods at 20 Hz, three periods at 30 Hz, six periods at 50 Hz and seven periods at 60 Hz. Obviously, the 40 Hz-SSR did not need to be cut. The Fourier series was performed on the recorded and

synthesized curves utilizing dedicated software which yielded amplitude, phase, a_n and b_n Fourier coefficients and a DC term a_0 at the requested frequencies. In order to keep the phase monotonically increasing with the stimulus repetition rate, we added 2π to phase values when needed (Hari et al., 1989).

T-paired test was performed in order to compare amplitude and phase values of the recorded and synthesized curves. Differences were considered significant at $P < 0.01$.

The significance of the slope of the regression line calculated on normalized phase and amplitude values (see results) was evaluated by *t*-test. The regression slope was considered significantly different from zero at $P < 0.01$.

3. Results

All our subjects showed clearly identifiable responses at each stimulus repetition rate (7.9, 20, 30, 40, 50, 60 Hz).

Grand averages of the auditory evoked responses from all subjects at each repetition rate are illustrated in Fig. 2 while grand averages of the synthetic responses obtained at 30, 40, 50 and 60 Hz are shown in Fig. 3. The recorded and synthetic steady-state responses showed a good synchronization at all tested repetition rates even though the highest amplitude was observed at 40 Hz.

Mean and standard deviations of amplitude and phase values from the recorded and synthetic SSRs are plotted in Fig. 4 as a function of the stimulus rate. The mean amplitude value obtained from the recorded responses was highest at 40 Hz ($0.65 \mu\text{v}$). At this rate, amplitude resulted about 1.5 times higher as that observed at 30 Hz ($0.44 \mu\text{v}$) and 3 times higher as that observed at 60 Hz ($0.21 \mu\text{v}$). Looking at individual values, twelve subjects showed the highest amplitude at 40 Hz, two subjects ($N = 7$ and 15) at 30 Hz and two subjects ($N = 1$ and 16) at 50 Hz (Fig. 5, left side).

Mean phase values calculated on the recorded SSRs increased when the stimulus rate was increased. This increase was linear from 30 Hz to 60 Hz while the inter-subject variability was small, particularly at 40 and 50 Hz (Fig. 4).

When considering synthetic responses (Fig. 4), we found that the amplitude/rate function appeared similar to that obtained from the recorded responses since the highest mean amplitude was observed at 40 Hz ($0.63 \mu\text{v}$). However, the mean amplitude at 30 Hz ($0.35 \mu\text{v}$) and mean amplitudes at 50 Hz ($0.56 \mu\text{v}$) and 60 Hz ($0.41 \mu\text{v}$) resulted respectively lower and higher compared to the mean amplitudes of the recorded responses at corresponding stimulus rates (30 Hz: $0.44 \mu\text{v}$; 50 Hz: $0.49 \mu\text{v}$; 60 Hz: $0.21 \mu\text{v}$). The difference

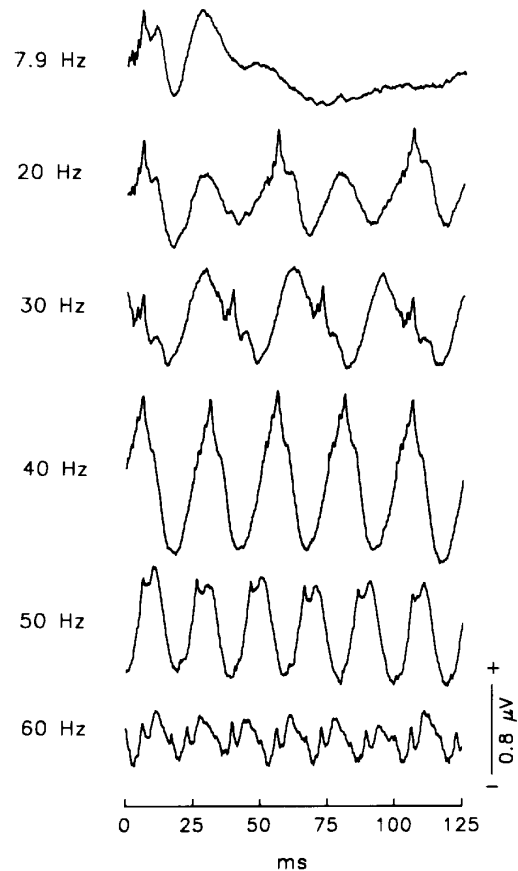


Fig. 2. Recorded steady-state responses. Auditory potentials recorded at stimulus rates of 7.9, 20, 30, 40, 50, 60 Hz are shown. Grand averages from all the tested subjects are reported.

between the actual and predicted amplitudes attained the significant level at 60 Hz ($P < 0.01$). With regard to individual values, ten subjects showed the highest amplitude at 40 Hz, one subject ($N = 11$) at 30 Hz and 5 subjects ($N = 5, 6, 7, 8$ and 12) at 50 Hz (Fig. 5, right side).

Mean phase values of the synthetic responses (Fig. 4) increased linearly when increasing the stimulus rate. The mean phase value obtained at 40 Hz (4.404 rad) was very close to that calculated for the recorded responses (4.504 rad). However, the mean phase at 30 Hz (3.016 rad) was lagging while mean phases at 50 (5.761 rad) and 60 Hz (6.980 rad) were leading in comparison to those obtained for the recorded responses at corresponding rates (30 Hz: 2.357 rad; 50 Hz: 6.162 rad; 60 Hz: 8.327 rad). The difference between the actual and predicted phase values was significant at 50 and 60 Hz ($P < 0.01$).

The behaviour of the recorded SSRs was evaluated in reference to the values one would expect if assuming

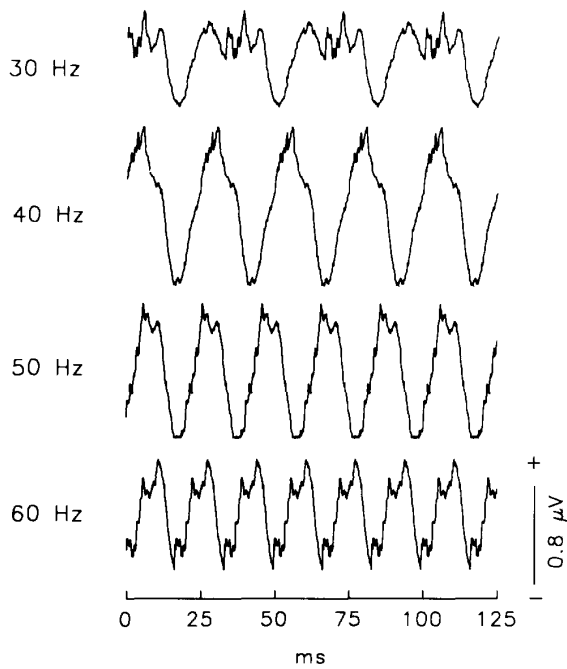


Fig. 3. Synthesized steady-state potentials. Auditory potentials synthesized at stimulus rates of 30, 40, 50, 60 Hz are shown. Grand averages from all the tested subjects are reported.

the linear superimposition of individual MLRs to generate the steady-state potentials. Thus amplitude and phase of the recorded curves were normalized with

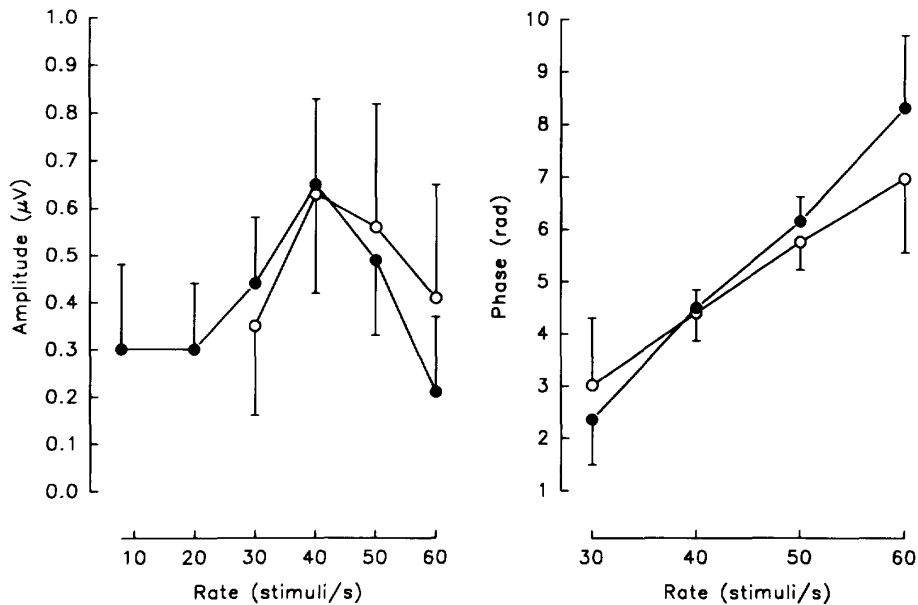


Fig. 4. Amplitude/rate and phase/rate functions of auditory potentials. Mean amplitude and phase values of the recorded (filled circles) and synthesized (empty circles) responses at different repetition rates (7.9, 20, 30, 40, 50, 60 Hz) are reported. Bars indicate one standard deviation.

respect to the corresponding values obtained from the predicted curves by subtracting the predicted values from the corresponding actual values. Individual and mean amplitude and phase normalized values are reported in Fig. 6. Normalized amplitude linearly decreased (regression coefficient = -0.0095 ; constant = 0.390 ; correlation coefficient = 0.633) when increasing the stimulus rate. Normalized phase values linearly increased when the stimulus repetition rate was increased (regression coefficient = 0.0632 ; constant = -2.547 ; correlation coefficient = 0.615). It should be remarked that the slope of the regression line significantly differs from zero with respect to both the amplitude (t -stat = -4.604 , $P < 0.0001$) and phase (t -stat = 4.324 , $P < 0.001$) normalized values.

4. Discussion

In our study we recorded the evoked potentials at several stimulus rates. Our results are in substantial agreement with previous reports since the highest amplitude of the responses was obtained at 40 Hz and the phase increased linearly from 30 Hz to 60 Hz (Galambos et al., 1981; Stapells et al., 1984; Hari et al., 1989). Previous studies reported also a depression in the amplitude/rate function at 25 Hz (Galambos et al., 1981; Stapells et al., 1984; Stapells et al., 1988) or 30 Hz (Hari et al., 1989) and an additional peak at 20 Hz (Galambos et al., 1981; Stapells et al., 1984; Hari et al.,

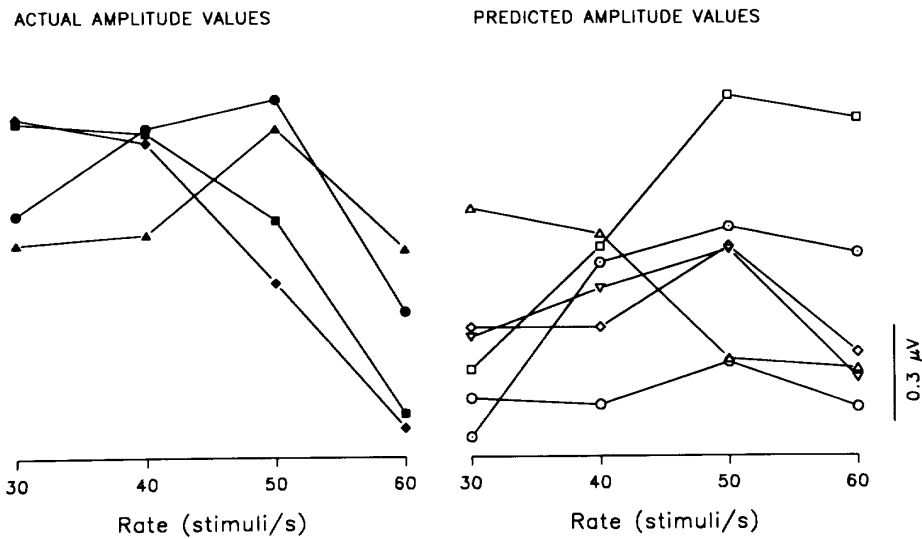


Fig. 5. Deviations from mean behaviour in amplitude/rate functions of steady-state responses. Individual amplitude/rate functions with maximum amplitude at frequencies other than 40 Hz are shown for the recorded (Subjects 1: ●, 7: ■, 15: ◆, 16: ▲) (left side) and synthetic (Subjects 5: ○, 6: □, 7: ⊙, 1,8: ◇, 11: △, 12: ▽) (right side) responses.

1989). These data, together with the amplitude enhancement observed at 40 Hz, have been taken to support the hypothesis of the linear MLR addition as the mechanism underlying the 40 Hz-SSR generation, given the periodicity and latency values of MLR components. However, we did not find either the additional peak at 20 Hz or the depression at 30 Hz in the

amplitude/rate function since mean amplitude values at 20 Hz and 30 Hz were respectively 46% and 68% of the mean amplitude obtained at 40 Hz. We are not able to give a clear explanation of these findings even though differences in stimulation and recording paradigms as well as in the measurement of the SSR amplitude should be taken into account to justify the

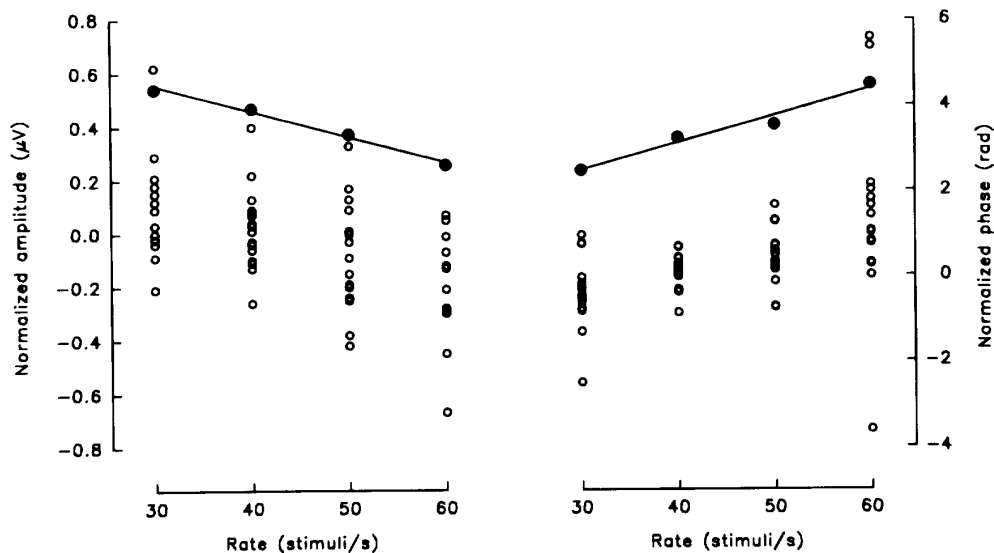


Fig. 6. Normalized amplitude and phase values of steady-state responses. Individual values (empty circles) of amplitude (left side) and phase (right side) of the recorded responses normalized with respect to the predicted ones are reported. Mean values (filled circles) and linear regression lines are shifted respectively by $0.45 \mu\text{V}$ (amplitude) and π (phase) along the vertical axis, for clarity.

discrepancies between our data and those obtained by others. Moreover, we did not record the responses at 25 Hz which is the rate associated with the amplitude depression in the amplitude/rate functions reported by Galambos et al. (1981) and by Stapells et al. (1984), (1988).

As previously reported (Galambos et al., 1981; Stapells et al., 1988; Hari et al., 1989; Plourde et al., 1991), the predicted 40 Hz-SSRs obtained utilizing MLR as the basic response showed mean amplitudes and phases very close to those of the recorded 40 Hz-SSRs. However several data point to a consistent difference between the recorded SSRs and the SSRs predicted on the basis of MLR addition.

Firstly, as individual observations are concerned, several subjects showed the highest amplitude at stimulus rates other than 40 Hz, and this finding is in agreement with individual data reported previously (Stapells et al., 1984; Hari et al., 1989). However these differences from the mean are not paralleled by corresponding behaviours in the amplitude/rate functions in the predicted SSRs series. Indeed even the reverse is true, since subjects whose synthetic SSRs do not show the maximum amplitude at 40 Hz have not any correspondence in the recorded series.

Most importantly, with regard to mean values, the predicted amplitude resulted lower at 30 Hz and higher at 50 and 60 Hz in comparison to the recorded one, even if the significance was attained only at 60 Hz. As far as the phase is concerned, the predicted curves had a mean phase value which was very close to that of the recorded one only at 40 Hz while they were lagging at 30 Hz and significantly leading at 50 and 60 Hz with respect to the recorded responses.

Normalized data describe the difference between the recorded SSRs and predicted SSRs and show that this difference consists in a linear amplitude decrease and a linear phase increase when the stimulus repetition rate was increased. The high level of significance of the regression coefficients points to a close dependence of the amplitude and phase of the recorded SSRs on the stimulus presentation rate. This clearly indicates a deviation of the SSR generating system from the linear behaviour.

Several studies have shown that a decrease in amplitude and an increase in latency when increasing the stimulus rate is a general property of evoked potentials. This property has been documented at suitable repetition rates for responses belonging to several classes of auditory evoked potentials (Davis et al., 1966; Rothman et al., 1970; Terkildsen et al., 1975; Hyde et al., 1976; Erwin and Buchwald, 1986; Suzuki et al., 1986; Kraus et al., 1988; Picton et al., 1992). Likewise, since phase values of the steady-state potentials can be regarded as related to the latency of the transient response components (Regan, 1989), it does not

seem unreasonable to argue that, in our study, the behaviour of the recorded responses is a result of specific rate effects dealing with the recovery cycle of the neural generators. These effects seem to take place starting from stimulus repetition rates lower than 40 Hz. As a consequence one should expect the amplitude and phase values of the recorded 40 Hz-SSR to be respectively lower and lagging in comparison with the predicted ones. On the contrary, according to previous reports, a close correspondence was found between the recorded and predicted SSRs. Therefore it can be assumed that other facilitating phenomena interact with adaptation to determine the parameters of the individual responses which coalesce to generate the surface-recorded SSRs. This issue is addressed and discussed in the companion paper.

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