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A NEURO-SYNAPTIC MODEL OF THE BILATERAL AUDITORY NERVOUS SYSTEM – IMAGE LATERALIZATION AND BINAURAL UNMASKING

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Summary

A model of bilateral interaction in the auditory nervous system was presented on the basis of the digital-chemical functions of neuro-synaptic circuits in order to analyze the mechanism of cross-correlational information processing for binaural unmasking as well as sound localization. The system was composed of a bilateral pair of auditory relay nuclei, i.e., the cochlear nuclei, superior olives, trapezoid bodies, and inferior colliculei, which are organized in a pair of afferent systems from the cochlear nucleus to the inferior colliculus, as well as an efferent system from the inferior colliculus to the cochlear nucleus. The model system could detect interaural differences using the interaction of excitatory and inhibitory postsynaptic potentials evoked on the LSO neurons by the respective ipsilateral and contralateral outputs of the cochlear nuclei. The equalization and cancelation (summation) processes of binaural information were explained as mechanisms of the threshold controls of the analog-to-digital conversion neurons in the cochlear nucleus by the data on the detected interaural difference from the superior olive, and of the superimposition of bilateral combined excitatory and inhibitory postsynaptic potentials elicited in the inferior collicei by the cochlear nuclei in the second (direct) afferent auditory system. The effect of binaural unmasking was simulated in the model as a binaural phase-difference filter in order to discuss the mechanism of directed attention in the egocentric perceptual field.

1. Introduction

The effective detection of a signal in noise or the improvement of the signal-to-noise-ratio is one of the main subjects in communication system research. In human communication, such improvement can be experienced as the 'cocktail party effect,' which is considered to be due to the coordination of multiple interactions in the audiovisual, bilateral, and perceptuomotor systems, etc.[14]

In auditory perception, the detectability of a signal in noise depends on the relationship between the signal and the noise both in spectrum and time domain.[23] Auditory masking, the phenomenon of an increase in the threshold for signal detection by adding noise (masker) to a signal, has been confirmed for various types of signals and maskers; for example, tones masked by tones,[8] noise masked by noise, speech masked by speech, tones masked by noise, tones masked by speech, noise masked by tones, noise masked by speech, speech masked by tones, and speech masked by noise.[17]

When the signal and masker are presented to both ears, the masking effect decreases in some conditions. This decrease in masking is called 'binaural unmasking,' which depends on the bilateral interaction of the auditory nervous system. The difference in detection thresholds of a signal in a masker presented monaurally and binaurally is referred to as the masking level difference (MLD). The MLD for a monaural tone in binaural noise with no interaural difference (denoted T(M|M)/T(M|0)) is approximately 6 dB, and in the case of a binaural signal with reversed polarity in binaural noise with no interaural difference, the MLD (T(M|M)/T(π|0)) shifts up to 12 dB. However, the antiphasic or homophasic presentation of a signal as well as noise shows no MLD, i.e., T($\pi|\pi$) = T(0|0) = T(M|M).[5]

Various types of models of the bilateral interaction in the auditory system have been proposed to explain binaural unmasking as well as sound localization. Durlach developed Kock's equalization and cancellation (EC) model for noise suppression. The EC model is based on two processes: that is, adjusting the binaural stimuli to equalize the masking components in both channels and subtracting the stimuli to cancel the masking components. In Durlach's model, the transformation for the equalization is performed by multiplying the stimulus with a random amplitude factor as well as by delaying the stimulus with random delay. The detector in the final stage selects an input with a maximum signal-to-noise ratio among the three inputs, i.e., the transformed-subtracted signal and the original signals to both ears.[4] Colburn proposed another model for bilateral interaction which consists of a binaural analyzer as well as an ideal decision maker like the "Webster-Jeffress model." In his model, an improvement of the signal-to-noise ratio is achieved by controlling the decision maker with data on the interaural difference from the binaural analyzer.[2]

The auditory system is well known to consist of many relay nuclei which receive inputs from lower nuclei or the cochlea and sends the information to higher nuclei or the auditory cortex. However, this ascending auditory system is paralleled by a system of efferent pathways, which have been regarded as subsystems for various functions, such as feedback organization, the peripheral gating mechanism, peripheral adaptation, reciprocal influences between the two ears, the trophic function, and the feed-forward system.[13] Dewson transected the COCB (crossed olivocochlear bundle), which is one of the major efferent pathways, to observe the efferent effects at the cochlea.[3] He found a disability for sound discrimination in noise. Pickles and Comis applied atropine sulfate locally to the cochlear nucleus to block selectively the efferent pathway from the superior olive to the cochlear nucleus.[16] They measured the raised thresholds of tone-pips masked by wide- and narrow-band noise, but not the raised absolute thresholds.

In this paper, Durlach's and Colburn's models will be examined at the neurosynaptic level to observe the effect of binaural unmasking on a digital-analogue circuit model of information processing in the bilateral auditory nervous system with bidirectional communication.

2. The model

The present model consists of bilateral groups of five relay nuclei, i.e., the anteroventral cochlear nucleus (VCN); the dorsolateral cochlear nucleus (DCN); the medial nucleus of the trapezoid body (NTB); the lateral superior olive (LSO); and the inferior colliculus (ICC). As seen in Fig. 1, these nuclei are bidirectionaly con-

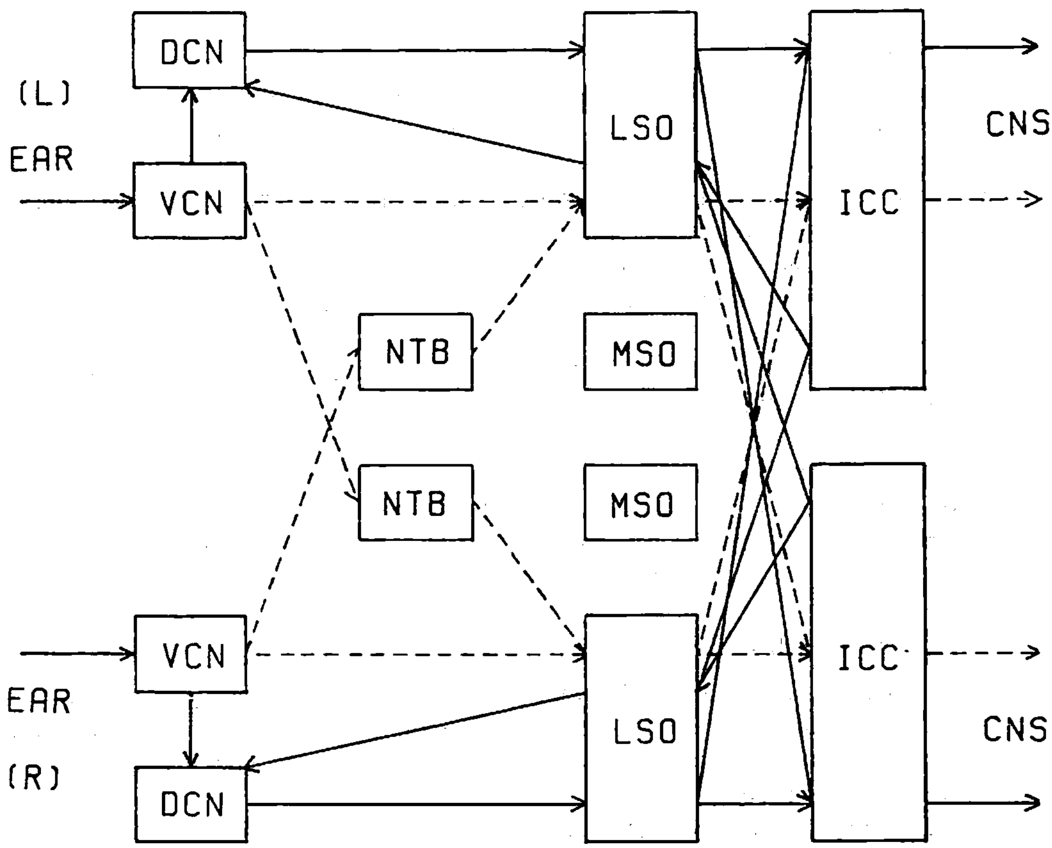

Fig. 1 *Block diagram of the bilateral auditory nervous system with afferent as well as efferent pathways. CNS: higher central nervous system (medial geniculate body, auditory cortex, etc.); DCN: dorsal cochlear nucleus; EAR: auditory input (via cochlear nerve); ICC: inferior colliculus; LSO: lateral superior olive; MSO: medial superior olive; NTB: medial nucleus of trapezoid body. Solid lines: pathways for EC process; dashed lines: pathways for D process.*

nected by afferent (solid lines) and efferent (dashed lines) pathways. The VCN, projected by the cochlear nerve, outputs to the ipsilateral LSO and contralateral NTB, which is connected to the LSO on the same side. The LSO sends output to both the ipsilateral and contralateral ICCs. The ICC also receives direct input from the contralateral DCN which receives auditory input through the VCN on the same side. These pathways to the ICC form a parallel afferent system. The ICCs, which are connected to each other, innervate the bilateral LSOs. The LSOs, then, innervate the DCNs on the same side, respectively.

Neuro-Synaptic Circuits

As mentioned in my previous paper,[9] the transmission of nervous pulses can be considered to occur by a series of conversions of digital to analogue signals and a reconversion to digital signals. This conversion and reconversion is performed by the synapses and cell bodies of neurons, respectively. The analogous post-synaptic potentials (PSPs) which are generated on the cell bodies by the synapses are classified into two basic types of monopolar potentials, i.e., positive (excitatory) PSP (EPSP) and negative (inhibitory) PSP (IPSP).[1] These EPSPs and IPSPs can be superimposed in proper neuron networks to form bipolar as well as monopolar potentials.

The simple circuit of three neurons in Fig. 2 is an example of a network which generates a bipolar PSP.[21] If the E-neuron receives an input, the neuron sends a burst of pulses to both the I- and O-neurons. The I-neuron is activated by the burst to output a new burst of pulses to the O-neuron. On the O-neuron, the two bursts of pulses from the E- and I-neurons generate the respective EPSP and IPSP, which are superimposed to generate a bipolar potential. The O-neuron outputs a burst of pulses if the potential exceeds the threshold of the neuron.

The behavior of the Model System

The model system deals with binaural information in three, i.e., the detection of the binaural difference (D-process), the equalization of the binaural inputs (E-process), and the cancellation of the nonsignal components in the equalized binaural inputs (C-process).

These three processes are performed as follows.

1) Each VCN receives a train of pulses with a density analogous to the acoustic wave of the input.
2) The VCN conducts a burst of pulses with a density corresponding to the input amplitude for the ipsilateral LSO as well as for the contralateral NTB, which acts as an inverter to discharge a burst of inhibitory pulses in the LSO on the same side.
3) The two bursts from the ipsilateral and contralateral VCN (via the NTB) cause the EPSP and IPSP on the LSO neurons, respectively.
4) The LSO generates a train of pulses corresponding to the positive peak amplitude of the combined potential of the EPSP and IPSP.
5) The ICC counts and compares the two pulse trains from the bilateral LSOs in reciprocal action to determine the laterality of the binaural image (D-process).[10]

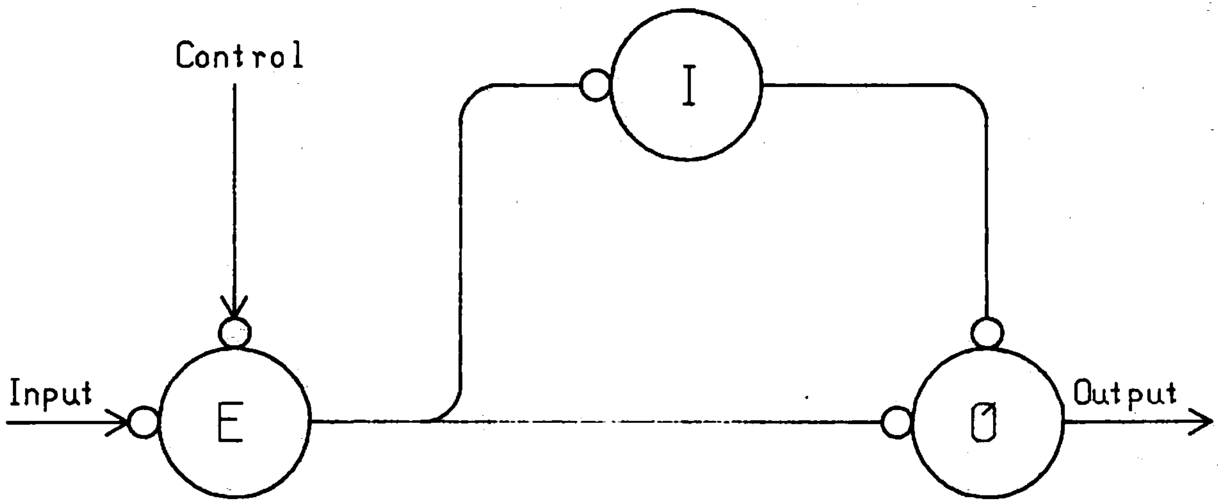

Fig. 2 *A simple neuronal network for generating a bipolar combined potential of excitatory (EPSP) and inhibitory (IPSP) postsynaptic potentials. E: input excitatory neuron with external 'control' signal of its threshold for analog(postsynaptic potentials)-to-digital (burst of pulses) conversion; I: inhibitory neuron; O: output neuron receiving excitatory pulses from the I-neuron as well as delayed inhibitory pulses from the I-neuron. A bipolar potential is evoked on the O-neuron, which generates a burst of pulses corresponding to the peak value of the combined potential of the EPSP and the delayed IPSP.*

6) The ICC on the side of the image lateralized, or the side of the larger LSO output, sends a train of excitatory pulses to the ipsilateral LSO as well as a train of inhibitory pulses to the contralateral LSO.
7) The LSO conducts a train of inhibitory/excitatory pulses in proportion to the LSO output to the ipsilateral DCN, according to the excitatory/inhibitory LSO output.
8) The LSO inhibitory/excitatory efferent pulses cause the upward/downward shift in the thresholds of the DCN neurons.
9) The DCN neurons, which receive a train of pulses analogous to the acoustical wave of the input from the ipsilateral VCN, respond transitively to generate a sequence of bursts containing the input intensity information as the pulse density, as well as the spectrum information as the repetitive frequency, of the bursts in the sequence.
10) The sequences from the DCNs on the side of the lateralized image and on the opposite side are, then, delayed and advanced in phase to equalize the neural timing of the binaural inputs (E-process).
11) The equalized sequence of pulse bursts from the DCN are sent to the contralateral LSO where the combined potential of the EPSP and IPSP is repetitively generated by each burst in the sequence.
12) The combined potential in each ICC is conducted to the opposite ICC to superimpose the two combined potentials.
13) The ICC neurons respond to the positive peak of the superimposed potential to send the output to the higher central nervous system.
14) Since the combined potential of the EPSP and IPSP is bipolar, the superimposed potential of the two combined potentials decreases in terms of its positive peak as the phase difference between the combined potentials increases (C-process).

Laterality Index

As mentioned in my previous paper (ref.), if the VCN neurons generate bursts of pulses with a density corresponding to the input intensity, the outputs of the bilateral LSOs as a pair of reciprocal peak detectors for the combined potentials of the EPSP and IPSP can be represented as follows;

$$L = \max(a_E . V_E(t) + a_I . V_I(t\text{-}d)) \tag{1}$$

$$R = \max(a_E . V_E(t\text{-}d) + a_I . V_I(t)) \tag{2}$$

where L and R are the left and right outputs; a_E and a_I are the intensity coefficients of the ipsilateral and contralateral inputs, respectively; and d is the interaural time delay.

The bilateral ICCs compare independently the two LSO outputs (L and R) to determine the laterality index, which is represented in terms of the normalized output of the ICC on the left (l) or right (r) side,

$$l = \begin{cases} \dfrac{L - R}{L_o + R_o} & (L \geq R) \\ 0 & (L < R) \end{cases} \tag{3}$$

$$r = \begin{cases} \dfrac{R - L}{R_o + L_o} & (R \geq L) \\ 0 & (R < L) \end{cases} \tag{4}$$

where L_o and R_o are the left and right LSO outputs for monaural presentation, respectively.

The Equalization Process

When the binaural inputs are sinusoidal waves, the optimal threshold control for equalization can be realized as follows.

If the binaural inputs to left ($S_L(t)$) and right ($S_R(t)$) ears have the interaural phase difference d, i.e.,

$$S_L(t) = \sin(pt) \tag{5}$$

$$S_R(t) = \sin(pt\text{-}d) \tag{6}$$

the optimal threshold shifts for the left (H_L) and right (H_R) inputs are

$$d = \min|\sin^{-1}(H_L)| + \min|\sin^{-1}(H_R)| \tag{7}$$

where H_L is positive and H_R is negative.

Combined potentials

In the present model, the time course for the EPSP ($V_E(t)$) or IPSP ($V_I(t)$) was simplified as follows,

$$V_E(t) = \begin{cases} \frac{1}{2}(1 - \cos 2\pi \frac{t}{2Tc}) & (0 \leq t < Tc) \\ e^{-(t-Tc)/\tau} & (Tc \leq t) \end{cases} \tag{8}$$

$$V_I(t) = -V_E(t) \tag{9}$$

where Tc is the duration of the conductance change and τ is the discharging time constant after the completion of the conductance change.

When the PSP is generated repetitively, the EPSP and IPSP are

$$V_E(t) = \begin{cases} \frac{1}{2}(1 - \cos 2\pi \frac{t}{2Tc}) & (0 \leq t < Tc) \\ (e^{-(t-Tc)/\tau})/(e^{-Tc/\tau} - e^{-T/\tau}) & (Tc \leq t < T) \end{cases} \tag{10}$$

$$V_E(t+T) = V_E(t) \qquad (T \leq t) \tag{11}$$

$$V_I(t) = -V_E(t) \tag{12}$$

where T is the time period of the repetitive stimuli.

The combined potential on the O-neuron in Fig. 1, $V_c(t)$ is described by

$$V_c(t) = n_E \cdot V_E(t) + n_I \cdot V_I(t-d_n) \qquad (13)$$

where n_E and n_I are the respective excitatory and inhibitory synaptic gains, and d_n is a neuron delay from the input to output.

Fig. 3 shows some examples of the combined potentials for $n_I/n_E = 0, 1, 2, 3$ and 5, and d_n = T/3, T/2 and 2T/3 in the case of the PSP charging duration Tc = T/3 and the discharging time constant τ = 2Tc.

3. Results

Phase Detection and Equalization in Steady-States

If each pair of parameters in the bilateral system is the same, the left and right systems work reciprocally. Fig. 4 shows the detectability of the interaural phase differences in binaural stimuli of the sinusoid (f = 1/T) balanced bilaterally in amplitude as well as in ability of equalization-cancellation in the case of the PSP charging duration Tc = T/3, the discharging time constant τ = 2Tc, the ratio of the inhibitory and excitatory synaptic gains n_I/n_E = 2, and the neuron delay d_n = 2Tc.

In Fig. 4, responses corresponding to two cycles of the repetitive stimuli are illustrated for nine examples of the interaural phase differences (IPD). The positive and negative waves in (A) represent the EPSP and IPSP evoked by the output bursts of the ipsilateral (left) and contralateral (right) (via NTB) VCNs. The upward and downward bars in (C) denote the left and right LSO outputs corresponding to the positive and negative peaks of the superimposed potential of the EPSP and IPSP in (B), respectively. The curve in (D) indicates the change in the laterality index as the IPD shifts from 0° to 360° (= 0°). The values 0, 1, and −1 of the laterality index correspond to the sound images located at center, left and right, respectively. In (E) are shown the threshold shifts of the DCNs in proportion to the LSO outputs in (C). The two waves represented by the solid and dashed lines in (F) indicate the combined potentials in the ICC caused by the equalized sequences of bursts from the left and right DCNs, respectively. The two potentials were superimposed as in (G), and the positive peak is plotted in (H). The plotted data in (H) were normalized by the peak value in the case of the monaural presentation. The peak values for less than 90° of the IPD maintain nearly 2.0 but show a tendency to decrease as the IPD exceeds 90°.

Phase-Difference Filter

Fig. 5, Fig. 6 and Fig. 7 show examples of the system responses under the same parameters as in Fig. 4 when the threshold control on the DCNs was fixed at the IPD levels 0°, 90° and 180°, respectively. The curves of each of the peak values in (H) had the characteristics of band-pass filters centered at 0°, 90° and 180° in the phase-difference domain, respectively.

The data suggest that the model system could act as a binaural filter in the interaural-phase domain.

Fig. 8 shows the change in the tuning curve of such a binaural filter as various parameters of the combined potential are adopted.

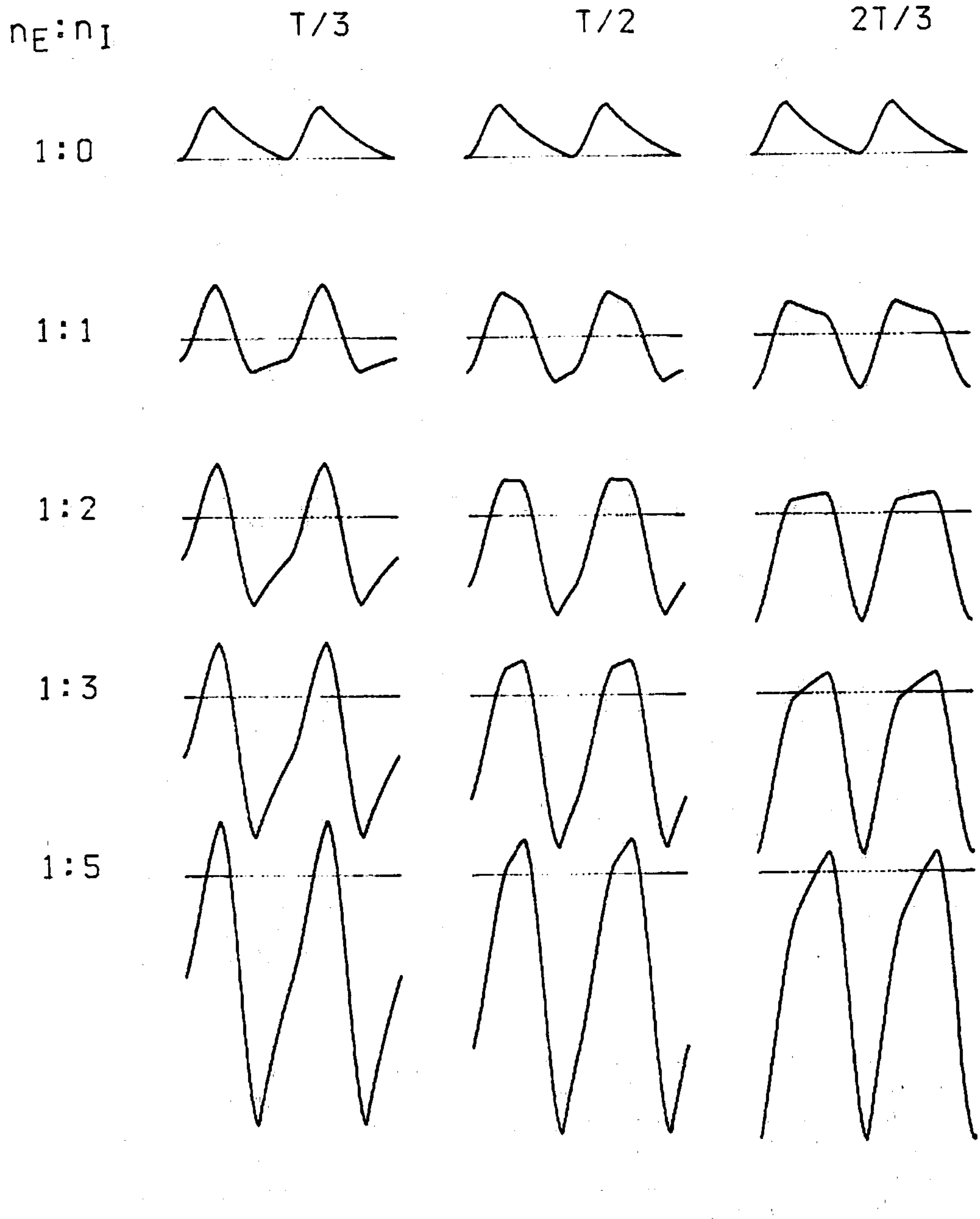

Fig. 3 *Examples of the combined potentials for the synaptic gain ratio* $n_I/n_E = 0, 1, 2, 3$ *and 5; and the neuron delay* $d_n = T/3, T/2$ *and* $2T/3$ *in the case of the PSP charging duration* $Tc = T/3$ *and the discharging time constant* $\tau = 2Tc$.

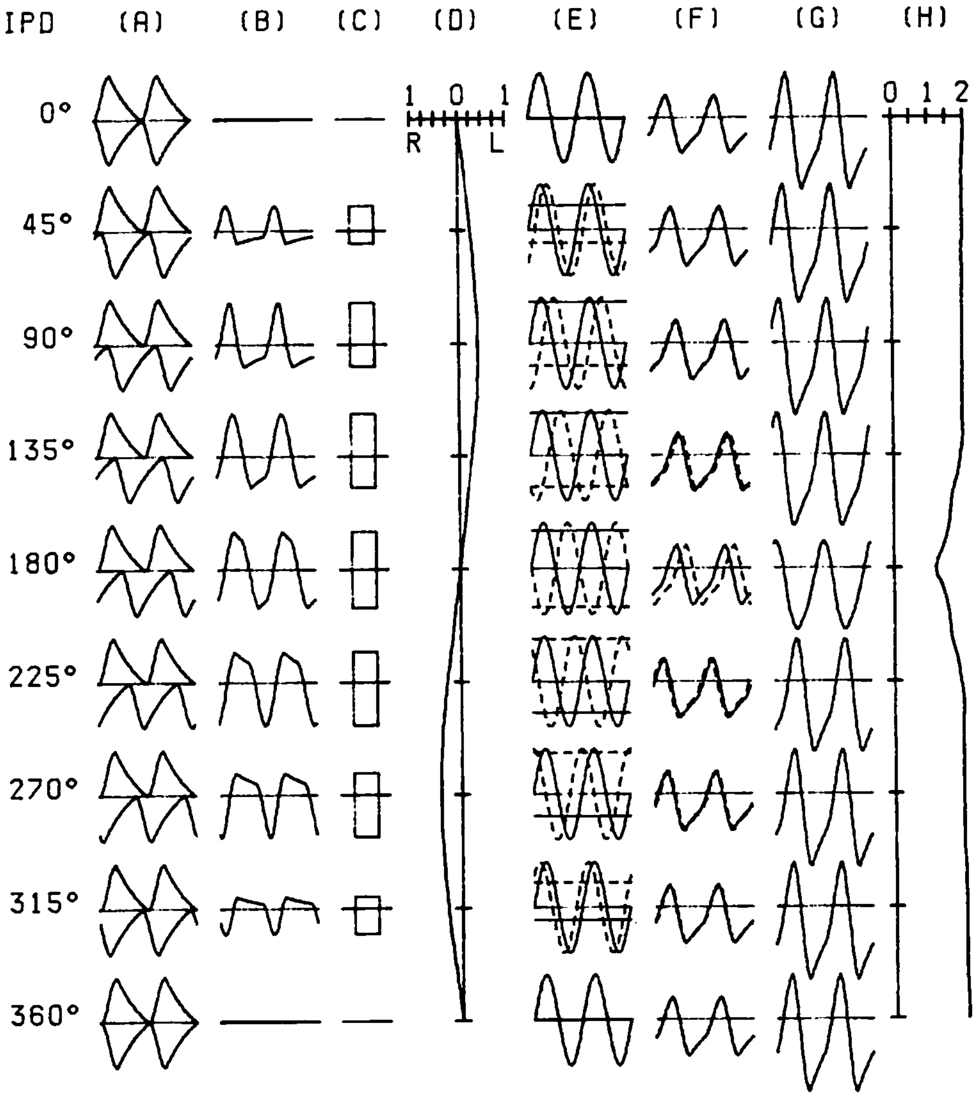

Fig. 4 *Steady-state response of the system for binaural stimuli of the sinusoid ($f = 1/T$), bilaterally balanced in amplitude, in the case of the PSP charging duration $Tc = T/3$, the discharging time constant $\tau = 2Tc$, the synaptic gain ratio $n_I/n_E = 2$, and the neuron delay $d_n = 2Tc$. IPD: interaural phase difference; (A): EPSP and IPSP evoked by the ipsilateral (left) and contralateral (right) (via NTB) VCNs; (B): superimposed potential of the EPSP and IPSP on LSO; (C): the left and right outputs corresponding to the positive (upward) and the negative (downward) peaks of the superimposed potential; (D): laterality index (1 div = 1/4 of the image position of a monaural stimulus); (E): input sinusoids and the shifted threshold of the left (upward) and right (downward) DCNs, respectively; (F): two combined potentials on the left (solid line) and right (dashed line) ICCs, respectively; (G): superimposed potential of two combined potentials from the left and right ICCs; (H): positive peak of the superimposed potential.*

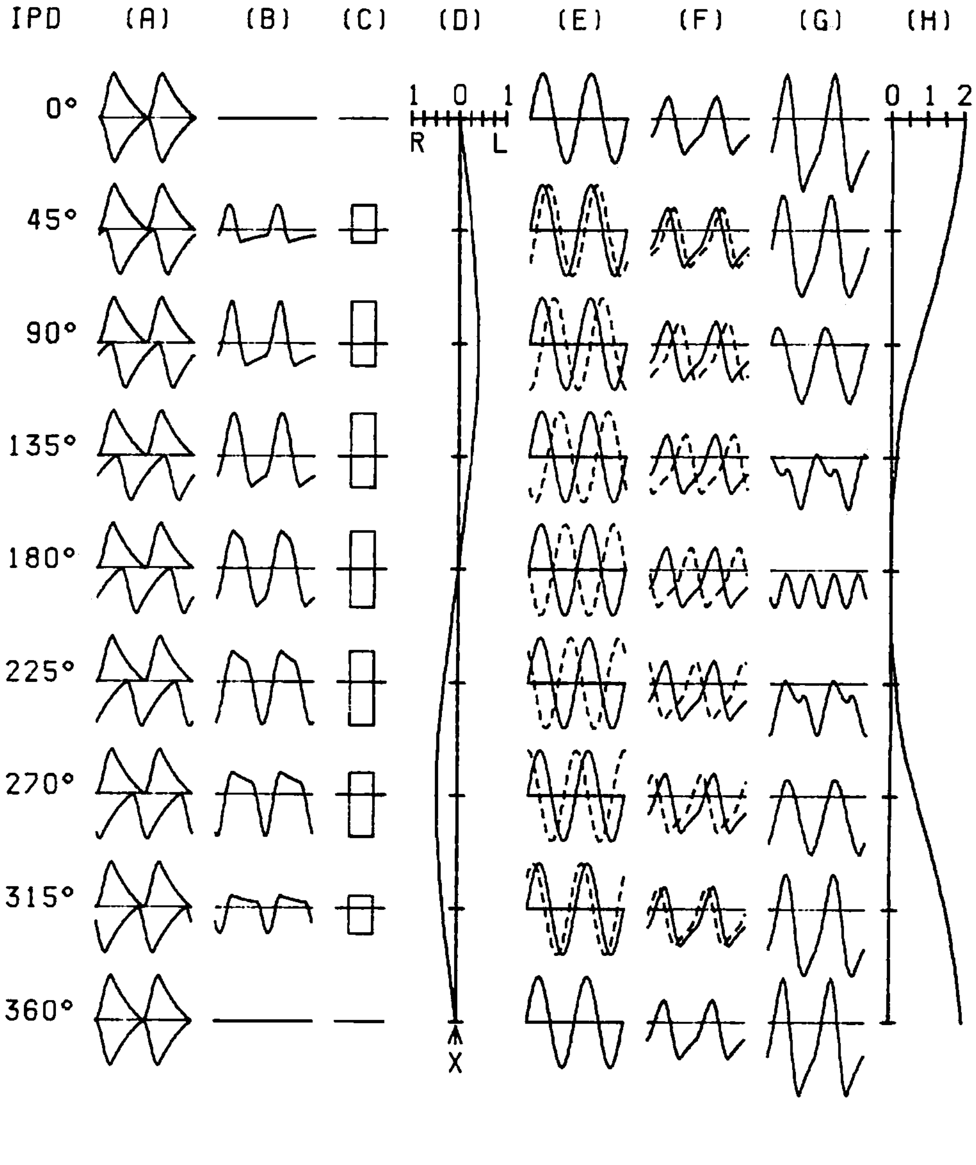

Fig. 5 *Steady-state response of the system under the same parameters as in Fig. 4 when the threshold control was fixed at the IPD level of 0°.*

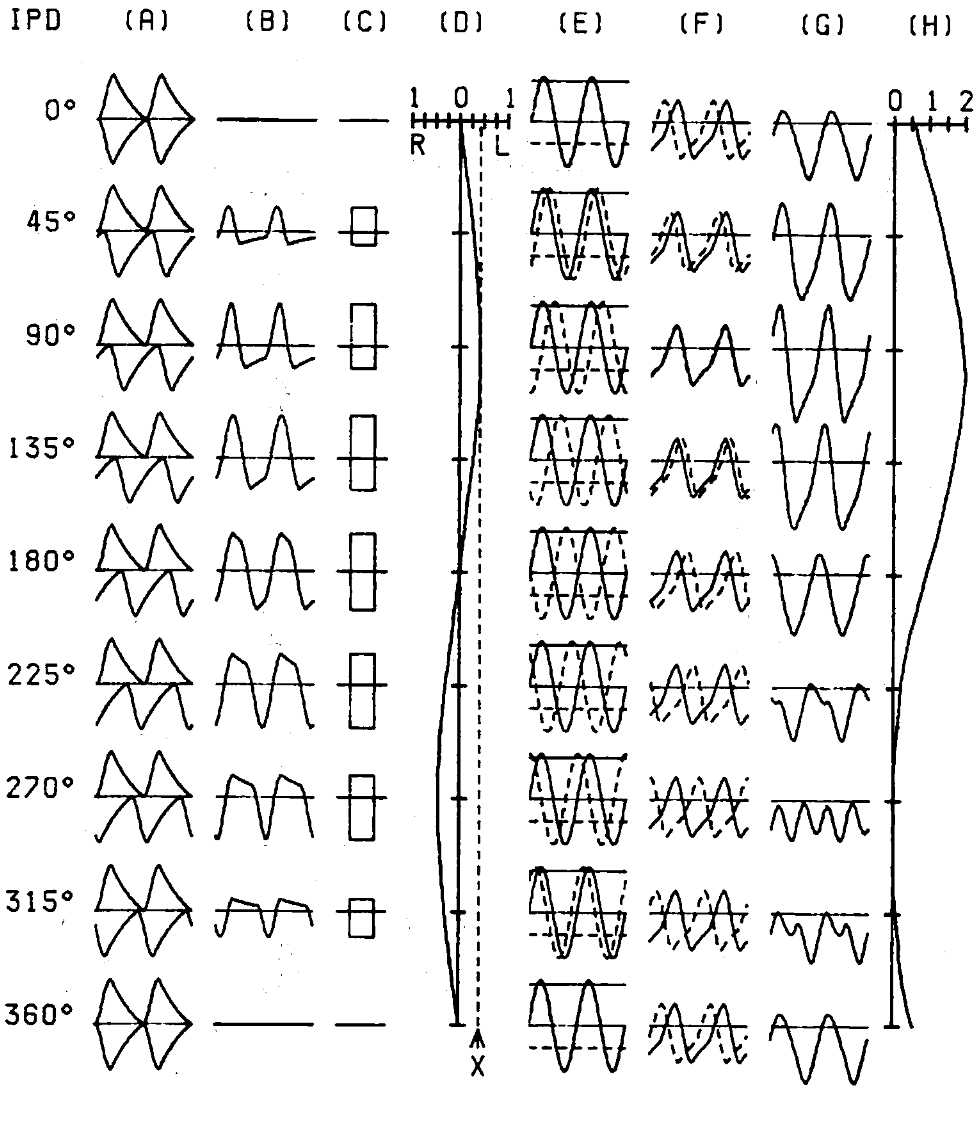

Fig. 6 *Steady-state response of the system under the same parameters as in Fig. 4 when the threshold control was fixed at the IPD level of 90°.*

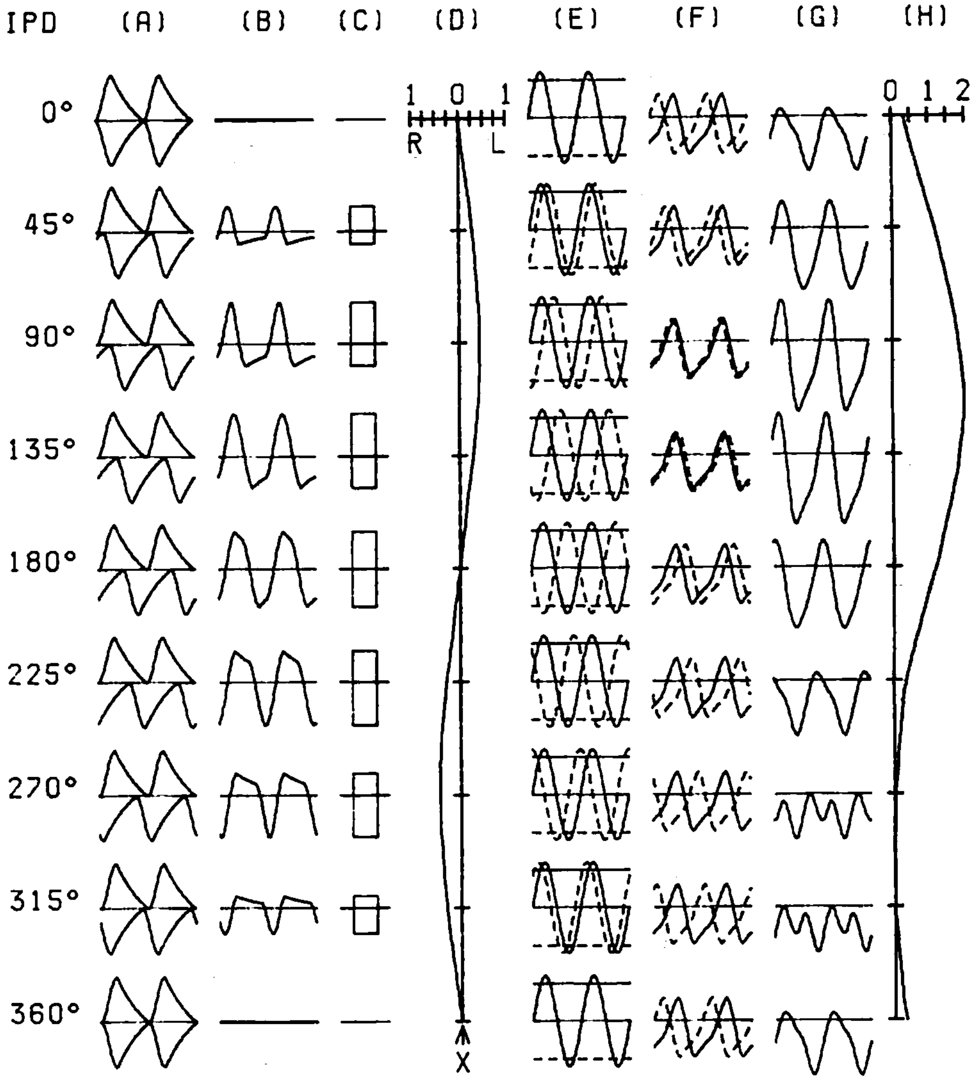

Fig. 7 *Steady-state response of the system under the same parameters as in Fig. 4 when the threshold control was fixed at the IPD level of 180°.*

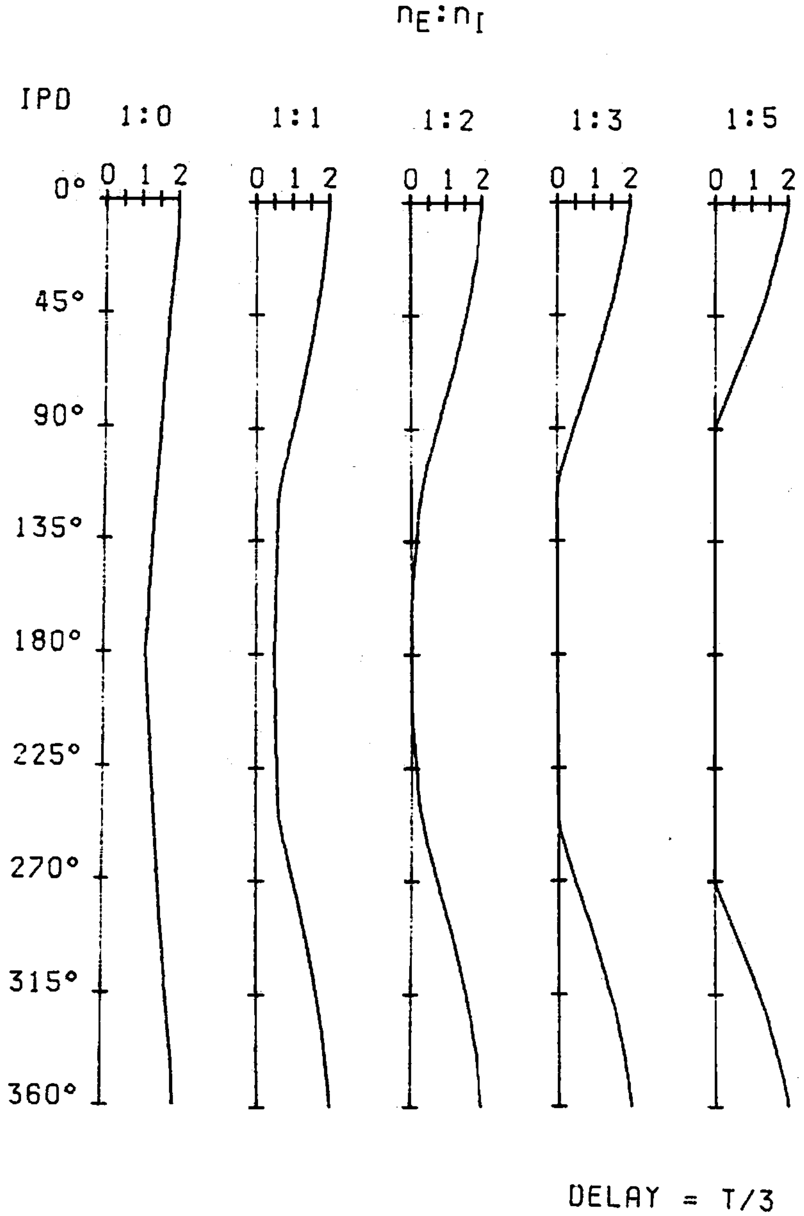

Fig. 8 *Peak values as in Fig. 4 (H) representing the change in the system response as the tuning curve of the binaural filter in the interaural phase-difference under various combined potentials.*

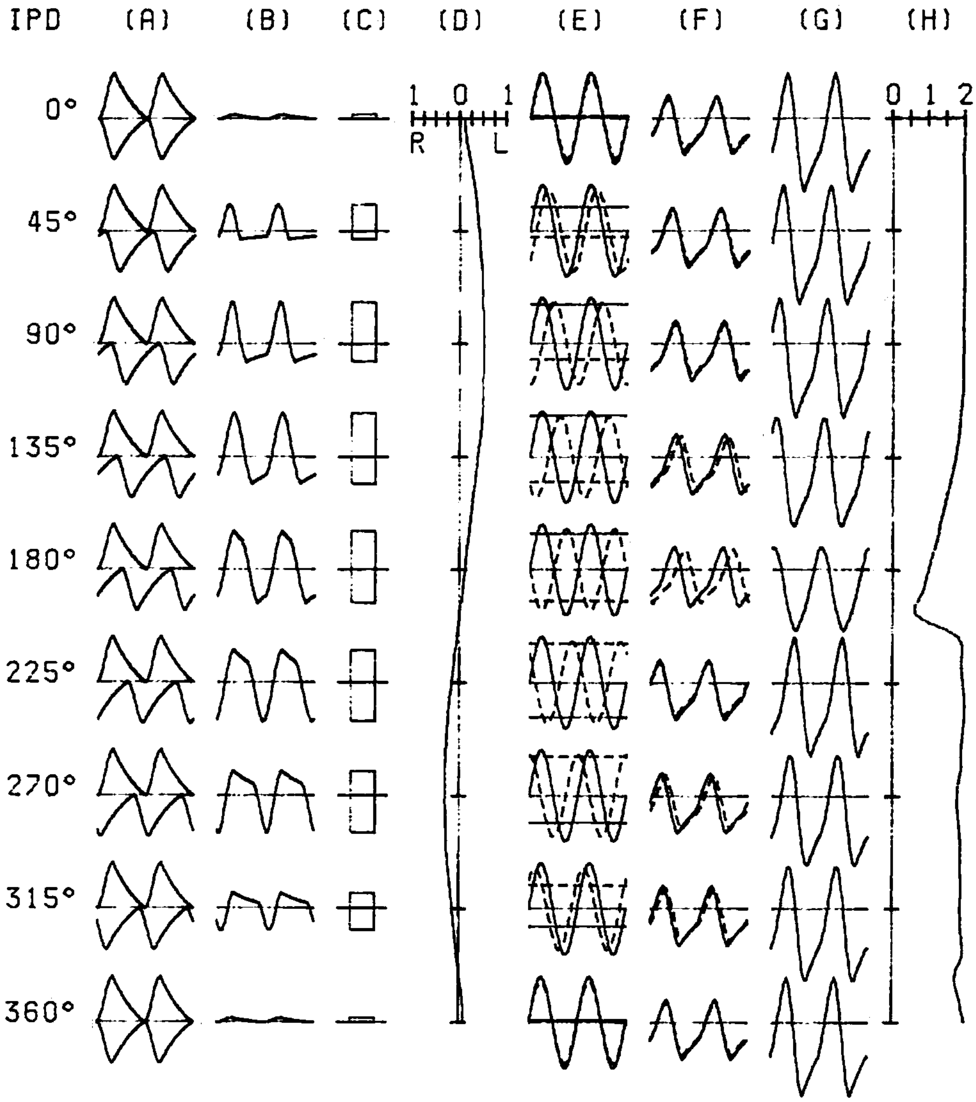

Fig. 9 *Steady-state response of the system for unbalanced binaural stimuli (a_I(right ear input)/a_E(left ear input) = .9).*

Phase-Intensity Trade

Fig. 9 shows an example of the steady-state response for binaural stimuli with an interaural intensity difference ($a_I/a_E = .90$) under the same parameters as in Fig. 4. The whole curve of the laterality index in (D) shifted toward the left with almost the same shape as in Fig. 4. The phase angle at the zero crossing point of the laterality index curve corresponds to the phase advantage of the right ear for centering the image of binaural input with unbalanced intensity. This is the 'phase-intensity trade.' The equalization process was performed even for IPD = 0°.

4. Discussion

A model of binaural interaction in the auditory nervous system was presented on the basis of the digital-analog functions of the neuro-synaptic circuits in order to analyze the mechanism of sound localization and binaural unmasking. The model could detect interaural differences using the interaction of the EPSP and IPSP to equalize and cancel the binaural inputs by threshold control of the analog-to-digital conversion and by the superimposition of the bilateral combined potentials of the EPSP and IPSP.

The present model is based on the analogous interaction of the EPSP and IPSP. In particular, the combined potentials can be obtained by the coordination of the excitatory and inhibitory neurons as in Fig. 2. Nelson and Erulker have shown that a click stimulus to one ear elicits a depolarizing potential in the inferior colliculus of the cat, while the same stimulus to the other ear produces a predominantly hyperpolarizing potential. On the basis of such experimental data, Erulker et al. presented three hypothetical patterns of synaptic activity elicited by transient binaural stimulation to explain the neuronal mechanism of sound localization.[6]

Recently, Segev and Parnas analyzed the nervous integration at the cellular level to conclude that under certain conditions, the maximal nonlinearity in the summation of PSPs is obtained with asynchronized activation of the two synaptic inputs rather than with simultaneous activation, and that the time integral of the voltage is more sensitive to the timing of the synaptic inputs than is the voltage amplitude.[19]

In the present model, the equalization process is performed by controlling the thresholds in the DCN neurons. Rose et al. observed phase-sensitive neurons with various thresholds in the anteroventral cochlear nucleus of the cat.[12] The threshold should be restricted at a certain level for obtaining the best binaural filter tuned to an interaural difference (a direction in the image space).[22]

Schwartz suggests that the MSO plays a role in the reflex movements of the eyes and head in response to the direction of sounds rather than binaural sound localization.[18] Synapse endings have been found with small vesicles which do not come from the auditory system but possibly from the visual system. If the MSO is the lowest system of audiovisual interaction, the MSO innervated by the visual system as well as the LSO innervated by the higher auditory system may play a role in the interaction between the sound localization and visual orientation used for directed attention in the egocentric perceptual field.[20]

The model system explains binaural unmasking but not monaural masking.

Northrop has proposed a neuro-synaptic model for signal-to-noise ratio improvement in the insect visual system.[15] Gibson and Hirsch have presented a psychoneural model of the monaural masking process.[7] Both of these models are composed of threshold-controllable neurons and efferent, non-linear control pathways. It is necessary to add another neuro-synaptic filter in the phase domain to the model presented in this paper to explain the mechanism of monaural unmasking as well as binaural unmasking together with their temporal and spectral characteristics.[11]

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