PERIPHERAL AUDITORY ADAPTATION AND FORWARD MASKING

H. Duifhuis and A. W. Bezemer

Biophysics Department, Rijksuniversiteit Groningen, and Institute for Perception Research, Eindhoven, the Netherlands

1. INTRODUCTION

Adaptation in responses in primary auditory nerve fibers is a well documented phenomenon. There is little or no evidence that it is present at the level of the hair cell receptor potential. Therefore, it is quite plausible that the underlying mechanism(s) originate at the synapse. An attractive model for this mechanism is implied in the several "depletion" models, which have in common that transmitter aspects (substance, or channels) can be employed at a higher rate than at which they are replenished (e.g., Schroeder and Hall, 1974; Eggermont, 1975; Furukawa et al., 1978). These models lead to a multiplicative adaptation model: the reduced response is the result of a reduced gain factor of the system. Several theoretical studies had proposed to treat adaptation as an aspect of an automatic gain control (Siebert and Gambardella, 1968; Duifhuis, 1972; Johannesma and Koldewijn, 1973; De Jongh, 1978). However, neurophysiological follow-up studies, in particular those examining responses to brief increments on a pedestal signal, casted serious doubt on the validity of this interpretation (e.g., Smith and Zwislocki, 1975; Harris, 1977; Prijs and Eggermont, 1981). These data are, insofar as envelopes are concerned, described more accurately with an additive adaptation model. Since neither interpretation described all aspects of the data it is a fortunate development that recent theories present attempts to incorporate both mechanisms (Furukawa et al., 1982; Smith and Brachman, 1982; Schwid and Geisler, 1982).

Since the discovery of auditory forward masking (de Maré, 1940) it was realized that this psychophysical phenomenon was related to adaptation effects, that was likely to be caused by recovery from the state of adaptation at the masker offset. Evidence in support of this view was presented by Harris (1977) and Bauer (1978). The problem of relating the two is that visual inspection of the recorded data does not lead to more than a qualitative relation of adaptation and forward masking. The quantitative relation requires the quantification of (central) decision rules. For simple psychophysical detection tasks these rules have been described successfully with optimum detectors operating on peripheral neural data (starting with Siebert, 1965).

The present study is limited to an examination of the implications of the antithetical models of adaptation (multiplicative or additive) regarding temporal masking. This analysis should be followed up with the examination of the predictions of the more recent theories, which, however, still contain several assumptions that need further verification.

2. PREDICTING SIMULTANEOUS AND FORWARD MASKING

The first step in the analysis is to describe the responses in peripheral auditory nerve fibers mathematically. As a basic framework we use De Jongh's (1978) model, a synthesis of many concurrent models of the peripheral auditory system. Figure 1a presents the (slightly modified) model. It is a multichannel model in which nonlinear interaction between channels is neglected. The model exhibits multiplicative adaptation, for the ease of analysis drawn here as a feedforward process. The modification towards additive adaptation is given in Fig. 1b. The major difference is that instead of multiplying $q_i(t)$, the output of $G_2$, by a factor $a_i(t)$, one decreases $q_i(t)$ by subtracting the quantity $d_i(t)$ (cf Smith, 1973; Prijs and Eggermont, 1981).
Fig 1a. One channel of De Jongh’s model of the peripheral auditory system, but with feed-forward instead of feedback adaptation/saturation, and a Poisson spike-generator rather than a trigger process (to simplify the analysis). The BPNL-section models cochlear filtering and nonlinearity; G2 is a half-wave rectifier; K limits synchronisation at high frequencies; Poisson process plus refractoriness actually constitute a Markov process. By taking $a_2(t) = (1 + \langle q_2(t) \rangle_T)^{-1}$, where $\langle \cdot \rangle_T$ implies averaging over a window $T$, the multiplicative adaptation model produces saturation. Fig. 1b. The additive adaptation model, specified for the envelope of the response but not for the fine structure; hence $E$; $T$ prevents the rate function $r_q(t)$ from being negative (linear half-wave rectifier). For $d_2$ one might take $d_2(t) = \beta \langle q_2(t) \rangle_T$ with $0 < \beta < 1$ (e.g., Smith, 1973).

Next we analyse the response to a probe in the vicinity of a masker. In this paper we limit ourselves to tonal stimuli: a masker M of duration $T$ and amplitude $A_M$, and a probe P with duration $\Delta T$ and amplitude $A_P$, presented at $t_P$ after masker onset, and masker as well as probe at $f=f_0$.

It is useful to make several other approximations in order to gain transparency, albeit at the cost of losing details. These simplifications do not alter the main conclusions which we will reach. The first approximation is to take

Fig. 2. Responses at successive points in the multiplicative and additive models to a tonal masker of duration $T$ and amplitude $A_M$ and a brief probe of duration $\Delta T$ and amplitude $A_P$, presented either simultaneously at $t_P$, or in the forward masking position $t_P'$. The bottom line shows the incremental responses to the probe as a function of its temporal location with respect to the masker. (The decrement in $r_{Pq}(t_P)$ in the simultaneous additive case is caused by the nonlinearities $G_1$ and $G_2$, not by adaptation.)