A computer model of medial efferent suppression in the mammalian auditory system

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Stimulation of the olivocochlear bundle reduces basilar membrane displacement, driven auditory nerve activity, and compound action potential (CAP) response to acoustic stimulation. These effects were simulated using a computer model of the auditory periphery. The model simulates the medial efferent activity by attenuating the basilar membrane response. The model was evaluated against three animal studies reporting measurements at three levels of the auditory system; basilar membrane, single auditory nerve fibers and whole auditory nerve CAP. The CAP data included conditions where tones were masked by noise and "unmasked" by stimulation of the olivocochlear bundle. The model was able to simulate the data both qualitatively and quantitatively. As a consequence, it may be a suitable platform for studying the contribution of the efferent system to auditory processing of more complex auditory sounds in distracting backgrounds.
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I. INTRODUCTION

The olivocochlear bundle is an important component of the mammalian auditory efferent system (Rasmussen, 1946). It originates in the superior olivary complex (SOC) and terminates in the cochlea. The purpose of this reflex appears to be the regulation of activity in the auditory nerve (AN) through modification of outer hair cell (OHC) electrical and mechanical properties and, more directly, through postsynaptic contacts on the AN itself. The efferent system is normally characterized as two separate olivocochlear systems, medial and lateral (MOC and LOC) according to their origin within the SOC. Although relatively little is known about the LOC system at present, the MOC system is much better understood and is known to act on the OHC so as to reduce the response of the basilar membrane (BM) to acoustic stimulation. The purpose of which may be to shift the dynamic range of hearing, reduce the effects of masking (unmasking), protect from sustained acoustic trauma and aid in selective attention (Rajan, 2000; Delgutte, 1990; Maison *et al.*, 2001).

Recent research (reviewed in Guinan, 2006) has considerably expanded our understanding of the physiology of the efferent system and has created favorable conditions for building models of how it functions. In this study we shall adapt an existing computer model of BM activity to simulate the effect of MOC efferent activity. Any change to the model BM response will necessarily have consequences for activity in the model AN.

The simulations reported here will replicate three empirical studies from different laboratories (BM: Russell and Murugasu, 1997; AN: Guinan and Stankovic, 1996; compound action potential (CAP): Dolan and Nuttall, 1988). The long term aim of the project is to use the modified model to study the functional role of the efferent system in auditory processing of complex stimuli such as music and speech (clean and with noise). The primary aim of this study, however, is to demonstrate that the new model, implementing the effect of MOC stimulation, is simply able to fit the physiological data demonstrated in each of these studies.

All three studies show that direct electrical stimulation of MOC fibers produces a reduction in the effect of acoustic stimulation. Russell and Murugasu (1997) showed that the displacement of the BM was reduced, whereas Guinan and Stankovic (1996) showed that AN activity was reduced and rate/level functions shifted toward higher intensities. Dolan and Nuttall (1988) showed a reduction in the CAP magnitude in response to efferent stimulation. They also showed a depression of the CAP response to a tone in a noise background. Intriguingly, they found that MOC stimulation reversed the suppressive effect of the noise leading to an *increase* in the CAP response. This increase confirms the same findings by Kawase and Liberman (1993) and is an example of MOC activity acting on the BM to enhance the response to stimuli presented in an adverse background. This *antimasking* effect is a particular challenge to the computer model.

In this study, an existing computer model of the response of the BM (Meddis *et al.*, 2001) was used after applying a simple modification to reflect the action of MOC activity. An attenuator was applied to the response of the BM so that the attenuation was proportional to the amount of MOC activity. This small change to the model structure was all that was necessary to simulate the physiological effects described. The BM model was then deployed as a component in a general model of the auditory periphery (Meddis, 2006) that simulated the response up to the level of the AN. In a study of speech perception, Ghitza *et al.* (2006) have recently suggested a similar modification to Goldstein's (1990) multiple band pass nonlinear model to achieve the same effect.

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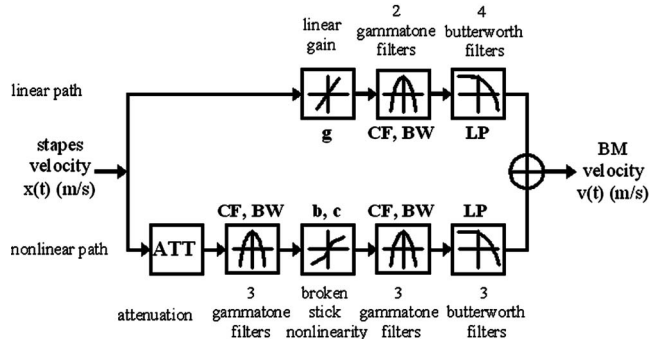
FIG. 1. Schematic of the modified DRNL filterbank. The modification involves the addition of an attenuation module (ATT) in the nonlinear path. Using ATT it is possible to use changes to a single parameter to simulate the suppressive effect of the efferent system. The amount of attenuation is determined by the amount of efferent activity. Parameters associated with each module are shown in bold letters.

It should be noted that the effect of MOC activity can be further subdivided into two processes (fast and slow) according to the time scales upon which they function (Sridhar *et al.*, 1995; Cooper and Guinan, 2003). The purpose of this paper is to model the basic suppressive effect of the MOC system and not to distinguish between these fast and slow systems at this stage. It is, however, reasonable to assume that the effect of the efferent system implemented in our model is the fast effect and is analogous to the effect of electrical shocks to the MOC observed in the studies replicated in the following.

II. THE COMPUTER MODEL

The computer model of the auditory periphery and its parameters are taken from Meddis (2006). It consists of a cascade of modules representing the resonances of the outer/middle ear, the response of the BM, the inner hair cell (IHC) stereocilia, the IHC receptor potential, calcium dynamics, transmitter release and adaptation at the IHC/AN synapse and the generation of AN action potentials. Unless specified, the model is the same in all respects to the detailed description given in the appendix of Meddis (2006) where the parameters are specific to the guinea pig.

The output from the model is a stochastic train of spikes in one or more simulated AN fibers. A schematic diagram of the dual resonance nonlinear (DRNL) BM model is given in Fig. 1. One of the resonances is linear (top) and the other nonlinear (bottom). The nonlinear path has a compressive nonlinearity interpolated between two second-order gammatone filters. The compressive nonlinearity is a broken-stick function where compression is applied only above a certain level. The output from the model is the sum of the two resonances. Detailed discussions of this algorithm can be found in Meddis *et al.* (2001) and 2003.

The novel feature of the model is the attenuator marked ATT at the input to the nonlinear path. The amount of attenuation applied is a free parameter in this study with a value of 0 dB in the absence of efferent activity. When simulating the BM response during MOC stimulation, its value is varied to provide the best fit to the data.
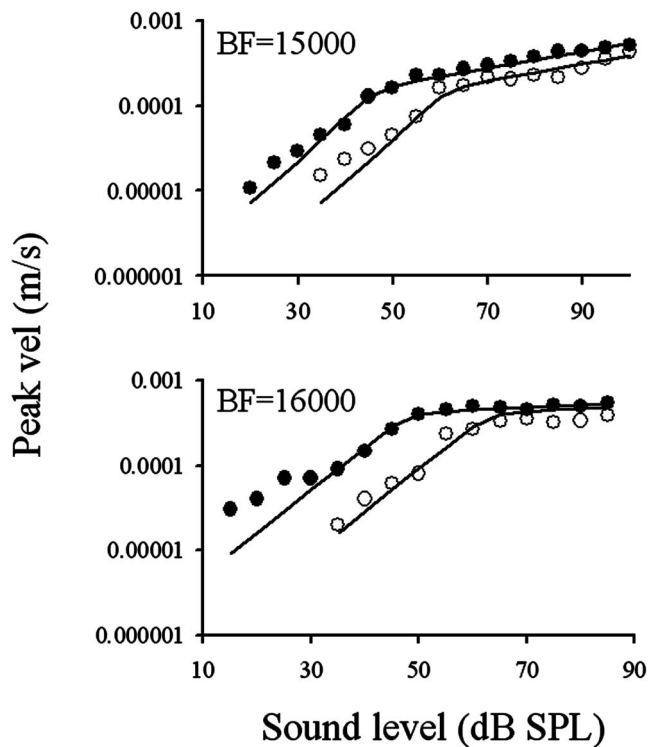

FIG. 2. Basilar membrane peak velocity (m/s) as a function of stimulus sound level for recording sites with BF of (A) 15 000 and (B) 16 000 Hz. Animal control data is shown as filled circles with the model control data as a line connecting these points. Measurements made during stimulation of the MOC are represented using unfilled circles and the model efferent data is shown as a line connecting the data points. Animal data is taken from Russell and Murugasu (1997). Model parameters are given in Table I.

The default parameters of all component modules are those used in Meddis (2006). Some of these parameters were developed in a series of studies by Sumner *et al.* (2002, 2003a, b). All computations were carried out using the MATLAB language and the code is available, on request, from the authors.

III. EVALUATION I: BASILAR MEMBRANE RESPONSE

Russell and Murugasu (1997) measured tone-evoked displacements of the BM in the basal turn of the guinea pig cochlea, with and without electrical stimulation of the olivocochlear bundle. They demonstrated that activation of the medial efferent system results in a reduction in the amount of basilar membrane displacement coupled with a shift of the rate-level function towards higher sound levels (see Fig. 2). Their data are plotted as individual points in Figs. 2(A) and 2(B) (control as filled circles and with MOC stimulation as unfilled circles). Results are shown for two experiments using measurements made at BM sites with BFs (best frequency) of 15 and 16 kHz. Their displacement measurements have been converted to peak velocity.

The data were simulated using a reduced version of the model incorporating only the outer/middle ear and BM functions. All relevant aspects of the animal experiments were replicated exactly. The stimulus was a BF pure tone with duration of 40 ms and rise and fall times of 2 ms. Stimuli were presented at levels ranging from 15 to 100 dB SPL in steps of 5 dB.

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TABLE I. Parameter changes required to fit the computer model response to the physiological data of Russell and Murugasu (1997).

Parameter	BF	
	15 000 Hz	16 000 Hz
a	600	1000
b	0.008	0.0025
c	0.2	0.05
ATT (dB)	15	15

A. Model parameters

Parameters were adjusted to provide the best fit to the model in two stages. First the model was adjusted to give the best fit to the control data [solid circles in Figs. 2(A) and 2(B)]. Parameters a and b were free to vary at this stage. Parameter a is the main determinant of the steeply rising slope to the left of the function. Parameter b is the main determinant of the shallow slope to the right of the function. Parameter g (linear path) was set to zero throughout, effectively reducing the model to a single (nonlinear) path. In the second stage, only the ATT parameter was adjusted to give the best fit to the BM measurements during stimulation of the MOC bundle [unfilled circles in Figs. 2(A) and 2(B)]. In this second stage, only the ATT parameter was changed. All parameter changes were guided by a criterion based on the least squares best fit between the model and experimental data. The resulting parameters are given in Table I. The model data are presented in Figs. 2(A) and 2(B) as lines connecting the animal data points.

B. Model results

Comparison of the animal and model data shows that a simple attenuation of the input to the nonlinear path of the model is adequate to model the observed shift in the rate/level function resulting from stimulation of the MOC. An attenuation of 15 dB was found to be optimal for both sets of data.

Although the fit between the model and the animal data was adequate along most of both functions, it is noteworthy that the animal control data could not be adequately fit at the lowest signal levels. The animal data is linear between 15 and 50 dB SPL but shows a reduced gain around 35 dB SPL in both sets of measurements. There is no provision in the model to simulate this. The discrepancy was not pursued as it was not directly relevant to the issue of efferent stimulation.

IV. EVALUATION II: AUDITORY NERVE RESPONSE

Guinan and Stankovic (1996) measured AN fiber responses in the cat for tone bursts with and without electrical stimulation of the olivocochlear bundle. They demonstrated that activation of the medial efferent system results in a shift in the rate level function to higher levels (see Fig. 3). The largest reductions in firing rate occurred in low and medium spontaneous rate fibers at moderate sound levels (45–75 dB SPL) with substantial reductions also present at around 100 dB SPL. Their data are plotted as individual points in Fig. 3 (control data are filled circles, whereas MOC stimulation data are unfilled circles). Results are shown for six ex-
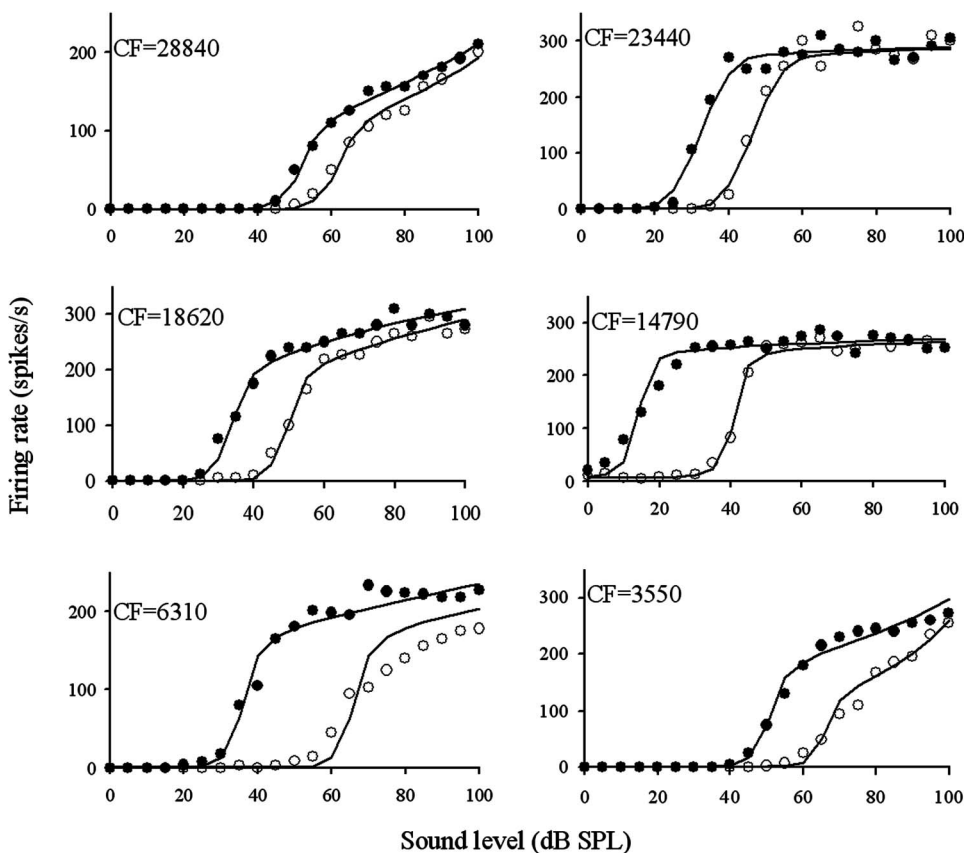

FIG. 3. Auditory nerve response (spikes/s) as a function of stimulus sound level (dB SPL). Individual figures show data from simulation of the model with stimuli of frequencies of 28 840, 23 440, 18 620, 14 790, 6310, and 3550 Hz for auditory nerve fibers with matching CFs (centre frequency). Animal control data is shown as filled circles with the model control data as a line connecting these points. Measurements made during stimulation of the MOC are represented using unfilled circles and the model efferent data is shown as line connecting these points. Animal data is taken from Guinan and Stankovic (1996). Model parameters are given in Table II.

TABLE II. Parameter changes used to fit the computer model to the animal data for the control (no MOC) condition (Guinan and Stankovic, 1996). ATT is the attenuation applied to the DRNL filter to simulate the effect of stimulation of the MOC bundle.

	CF					
Parameter	28 840 Hz	23 440 Hz	18 620 Hz	14 790 Hz	6310 Hz	3550 Hz
a	27 750	170 000	56 000	150 000	23 000	4500
b	0.165	0.6	0.092	0.018	0.012	0.014
G_{lin}	25	0	0	0	0	20
c	0.1	0.1	0.1	0.05	0.05	0.1
M	10	8	10	8	10	10
tauCa	0.00009	0.00015	0.00015	0.0004	0.00015	0.00015
ATT (dB)	10	14	16	27	30	23

periments using measurements recorded from auditory nerve fibers with CFs (centre frequency) of 28840, 23440, 18620, 14790, 6310 and 3550 Hz.

Although their results are qualitatively similar to that of Russell and Murugasu (1997), there are some important differences. The effect of MOC stimulation on the BM response was relatively simple and was similar for the two measurements reported previously. The data of Guinan and Stankovic (1996), however, show substantially different patterns of change for each fiber. No two fibers appear to respond in the same way. Given that the model aims to simulate MOC stimulation by changing only one parameter, it might appear unlikely that this would prove adequate to simulate the full variety of the animal AN data. In fact that is all that is necessary.

The computer model used to simulate the data of Guinan and Stankovic (1996) used the full range of peripheral modules; outer/middle ear, BM, IHC and AN responses. Their experimental protocol was followed as closely as possible. The stimuli were CF pure tones with a duration of 50 ms and rise and fall times of 2.5 ms. Stimuli were presented at levels ranging from 0 to 100 dB SPL in steps of 5 dB.

Guinan and Stankovic (1996) presented tones in succession, separated by 50 ms of silence. To reduce computational load, we evaluated the response of a cohort of 20 fibers with identical characteristics computed in parallel. As a consequence, our method does not include any cumulative adaptation that may have occurred in the animal recordings. Spike rates are based on a total count of all spikes occurring during the presentation of the stimulus.

A. Model parameters

The process of fitting the model parameters to the animal data proceeded in two stages in the same manner as described for the Russell and Murugasu (1997) data above. First, a range of parameters were adjusted to find a best-fit to the animal control data (filled circles in Fig. 3). In the second stage only the attenuation parameter (ATT) was changed to simulate the effect of MOC stimulation (unfilled circles in Fig. 3). All parameters of the model, before modification, are based on Meddis (2006). Table II shows only those parameters that were changed during the course of fitting the model to the data.

In the first stage we adopted various strategies to minimize the number of parameters that needed to be explored.

The gain, g, of the linear path in the BM model normally influences the output of the model only at high signal levels. This parameter was set to zero unless evidence was found of a change in slope of the rate/level function at very high signal levels. Parameter b, the BM gain above the compression threshold, does not influence the AN fiber rate if the fiber saturates at a signal level below that threshold. For two fibers (CF=14 790 and 23 440 Hz) it can be ignored. No changes were made to the compression exponent, c, of the model. Component bandwidths do not influence the model when measurements are made at BF and these were left at their default values. As a result, once the BF of the fiber had been set, only parameters a, b and, sometimes, g were changed in the BM component of the peripheral model. The only other parameters to be changed concerned the IHC/AN synapse. These were m (the maximum number of transmitter vesicles in the IHC/AN synapse) and tauCa (the time constant of clearance of IHC pre-synaptic calcium). The parameter m has a small effect on the saturated firing rate of the model fiber. The parameter tauCa is used to control the spontaneous rate of the fiber. The parameters used for each of the six simulations are given in Table II. The model data are presented in Fig. 3 as lines connecting the animal data points.

B. Model results

Comparison of the animal and model data shows that despite some imperfections, an acceptable fit was achieved in all cases for the purpose of studying the effect of MOC stimulation. The line connecting the unfilled circles shows the effect of attenuating the input to the BM model in order to simulate the effect of MOC stimulation. To achieve a good fit attenuations were required in the region of 10–30 dB (mean=19 dB). This is comparable to an attenuation of 15 dB required to simulate the data of Russell and Murugasu (1997). Four of the six evaluations give an excellent simulation of the effect of MOC stimulation. The two simulations at 6310 and 3550 Hz are probably acceptable but fail to replicate an apparent reduction in rate/level slope after MOC stimulation. This may, however, be the result of an initially imperfect fit to the control condition despite our best efforts.

V. EVALUATION III: CAP RESPONSE

Dolan and Nuttall (1988) recorded CAP responses to brief tones in silence and noise, with and without electrical
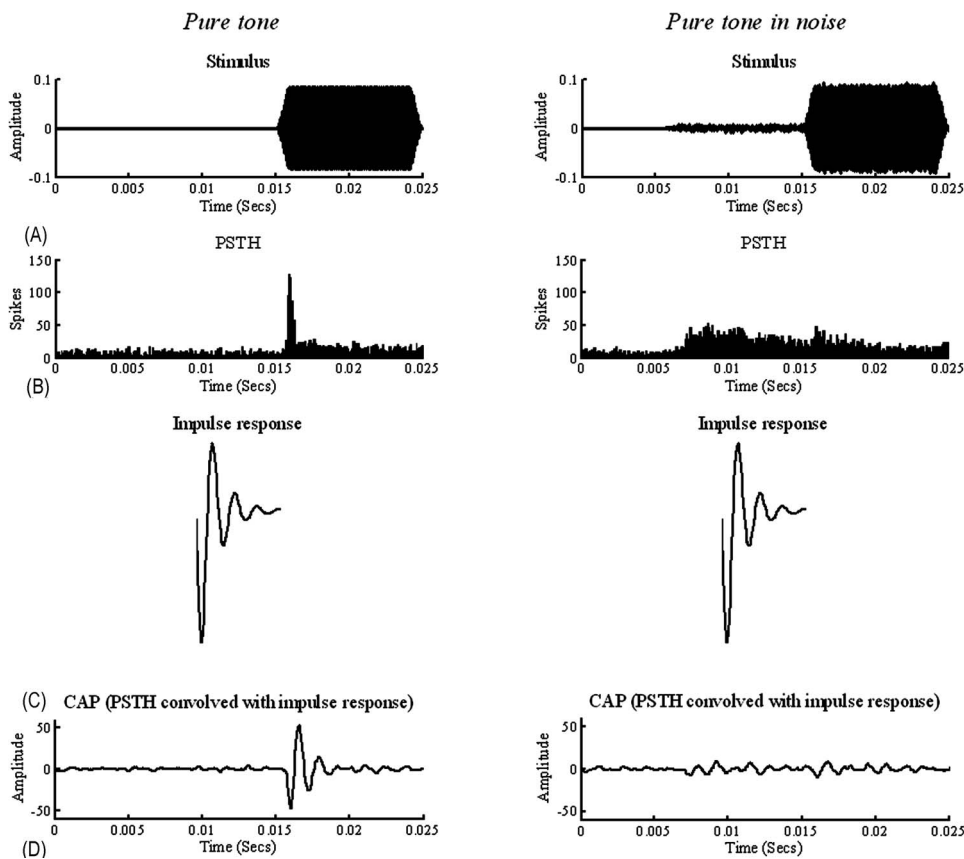
FIG. 4. Method used to simulate the auditory nerve compound action potential (CAP). (Left) Pure tone in silence and (right) pure tone in noise. (A) Initial stimulus. (B) The PSTH output from the auditory nerve stage of the model. (C) Impulse response as defined by Chertoff [2004, Eq. (3)] and (D) final peak CAP for the model during presentation of the tone after each spike in the (B) PSTH has been convolved with the (C) impulse response.

stimulation of the crossed olivocochlear bundle (see Fig. 5). They demonstrated that activation of the medial efferent system produces a shift to higher levels in the rate level function for tones, as demonstrated by Guinan and Stankovic (1996) and Russell and Murugasu (1997). When noise was added to the tones the CAP was reduced, presumably as a consequence of the adaptation caused by the noise. Dolan and Nuttall then demonstrated a partial restoration in the magnitude of the CAP response to tones in noise during MOC stimulation. This latter result is of considerable functional significance because it appears to represent an example of "unmasking" by efferent activity (Kawase and Liberman, 1993; Kawase et al., 1993).

Our simulation of the data of Dolan and Nuttall (1988) used the full model of the auditory periphery including outer/middle ear, BM, IHC, and AN. Parameters for the guinea pig auditory periphery as used for Evaluation II were also used. Because CAP reflects synchronized activity in the AN as a whole, a multi-channel version of the model was implemented with fibers arranged across 30 channels with BFs distributed on a logarithmic scale between 1 and 20 kHz. Each channel had 50 fibers with identical parameters making a total of 1500 fibers altogether. The CAP from the model was computed by substituting every AN spike [across all channels in response to a tone stimulus—Fig. 4(A)] with a single unit impulse response as defined by Chertoff [2004, Eq. (3)]. The result of this is that for every spike in the auditory nerve poststimulus time histogram [PSTH, Fig. 4(B)] we add the impulse response illustrated in Fig. 4(C). Because of synchrony and desynchrony in the firing of each of the auditory nerve fibers the addition of each of these

impulse responses either adds up, or cancels out. This is particularly evident in Fig. 4(D) where synchrony as a result of the tone onset produces a large impulse/CAP response. The CAP measure used was the maximum height of the CAP function measured during the presentation of the tone.

The experimental protocol of Dolan and Nuttall (1988) was followed as closely as possible. Stimuli were brief pure tones with a duration of 10 ms, and rise and fall times of 1 ms. They were presented at levels ranging from 30 to 80 dB SPL. The broadband (white) noise (BBN) had a duration of 20 ms and rise and fall times of 2 ms. It began 5 ms before and ended 5 ms after the tone. The noise was delivered at one of three different levels (21, 26.5, and 31 dB SPL rms) according to the experimental data being simulated.

In total, three simulations were performed (one for each of the three noise masker levels) as for the original study. Four conditions were performed in each simulation: (i) tone alone, (ii) tone in noise, (iii) tone alone with MOC stimulation, and (iv) tone in noise with MOC stimulation.

A. Model parameters

Parameter adjustment was carried out in two stages as for the previous two simulations. In the first stage parameters were chosen to obtain a good fit to the rate/level functions in both the control conditions (tone alone and tone with noise). These parameters were then used without alteration for all conditions including all three noise levels. MOC stimulation was simulated by changing the ATT in the nonlinear path of the BM (see Fig. 1). An attenuation of 8.4 dB was used in all conditions when MOC stimulation was indicated. The pa-

TABLE III. Parameter changes used to fit the computer model response to the physiological data of Dolan and Nuttall (1988).

Parameter	
StapesScalar	$5.5E-5$
$\log(BWnl)$	$=1.0+0.70^*\text{BF}$
ATT (dB)	8.4

rameter set began with the parameters given in Meddis (2006). Only two parameters required changing. The scalar applied to the stapes velocity was adjusted slightly from $1.4E-4$ to $5.5E-5$ to produce what is effectively a level adjustment of -8.1 dB. The parameters of the formula for computing the component bandwidths of the gammatone filters in the nonlinear path of the DRNL were adjusted to make the tuning curves of the individual channels slightly wider. The resulting parameters are given in Table III.

B. Model results

Figure 5 illustrates model and animal rate/level functions for auditory nerve fiber CAP magnitudes for noise masker levels of 21, 26.5, and 31 dB SPL. Animal data [Fig. 5 (left)] and model data [Fig. 5 (right)] are shown side by side for easier comparison. Data illustrated by unfilled circles shows data for the control condition (without BBN noise and without olivocochlear bundle stimulation). Data illustrated by unfilled squares shows data for the "BBN" condition (with noise masker and without olivocochlear bundle stimu-

lation). Data illustrated by filled circles shows data for the 'COCB' condition (without BBN noise and with olivocochlear bundle stimulation). Data illustrated by filled squares are for the "BBN + COCB" condition (with noise masker and with olivocochlear bundle stimulation). The model produced a useful qualitative fit throughout and a good quantitative fit. For noise levels of 21, 26.5, and 31 dB average correlations between the data and model results (across all four conditions) were 0.98, 0.98, and 0.97, respectively.

The effect of the MOC stimulation was an overall reduction in the observed CAP. This is consistent with the data reported earlier for the BM and AN. When noise was added to the tone the CAP was also reduced. This is a consequence of adaptation in the auditory nerve firing caused by the noise. The interesting result is the increase in the CAP for tones in noise (filled squares) when MOC stimulation is applied (filled squares). This occurs because the attenuation applied (to simulate MOC stimulation) reduces the response to the noise. This reduction in response reduces adaptation at the IHC synapse and also may cause desynchronization of the auditory nerve activity. As a result of the reduced activity in the system it is then possible for the presence of the tone to evoke a greater response.

VI. DISCUSSION

The main aim of this study was to evaluate a model of the auditory periphery with respect to its capacity to simulate the effect of MOC stimulation. The model is the same as an
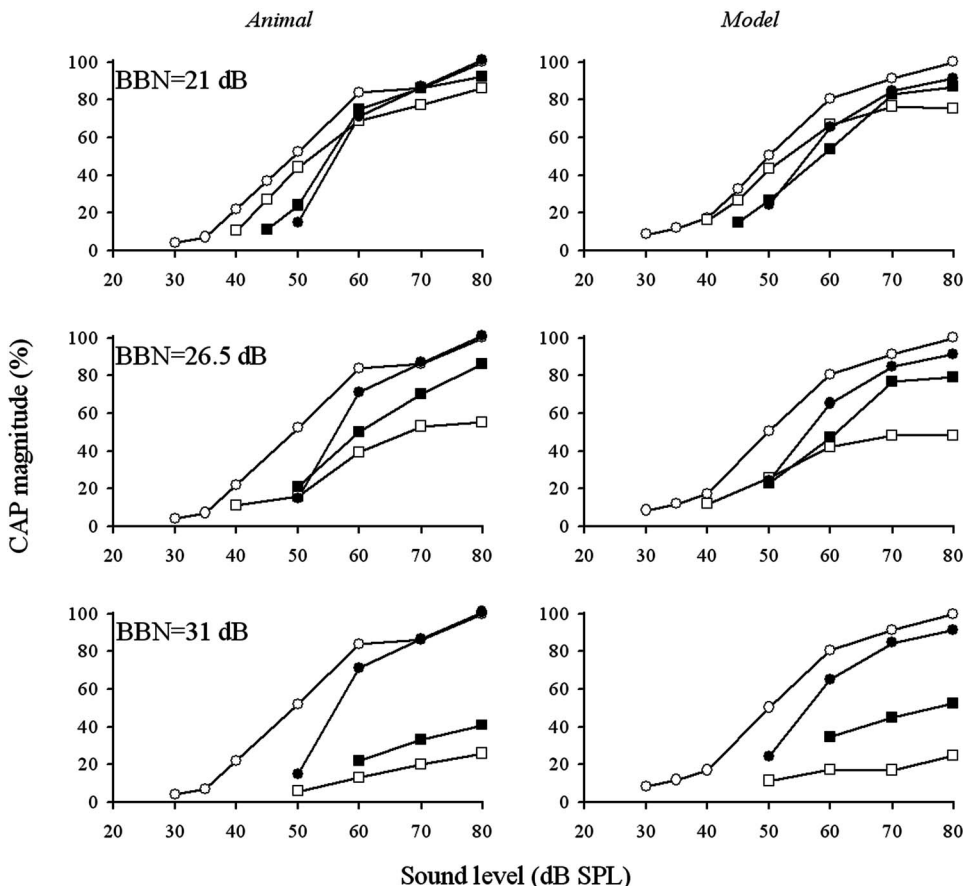

FIG. 5. Auditory nerve compound action potential (CAP) magnitude as a function of (left) stimulus sound level for the animal data and (right) model response. Graph shows the CAP magnitude in response to a 10 kHz tone alone ($\bigcirc$), a tone in the presence of broadband noise ($\square$), a tone alone whilst stimulating the crossed olivocochlear bundle ($\bullet$) and a tone in the presence of broadband noise whilst stimulating the crossed olivocochlear bundle ($\blacksquare$). Noise levels used are 21, 26.5, and 31 dB SPL. Animal data is taken from Dolan and Nolan (1998). Model parameters are given in Table III.

existing model except for the addition of an attenuator (Fig. 1—ATT) in the nonlinear path of the DRNL module used to simulate the response of the BM. The evaluations involved simulations of animal data collected in different laboratories at three different levels of the auditory periphery (BM, AN, and CAP responses) during stimulation of the medial olivo-cochlear bundle. The simulations were qualitatively and quantitatively satisfactory. The attenuation required to simulate the observed effects differed between simulations across a range of 7–30 dB. It is possible that these differences can be understood in terms of the different methods used to stimulate the MOC bundle but the published reports do not allow a direct comparison.

Our original expectation was that the algorithm to simulate MOC stimulation would be more complex than a single attenuator. The attenuator was initially positioned prior to both the linear and nonlinear pathways of the DRNL filterbank, this resulted in an overall signal level reduction. Using a Euclidean distance measure of best fit we were able to determine that this method provided as good a fit to the BM data of Russell and Murugasu (1997) as the present method. When we modeled the AN response of Guinan and Stankovic (1996) the model fit to the animal data was worse, particularly at higher signal levels. Moving the attenuator so that it applied only to the nonlinear path rectified this and produced a good fit with the animal data, notably at higher signal levels where it had previously failed to fit for the AN data. As a result of our original approach failing to account for efferent effects it seems necessary that MOC attenuation acts on the nonlinear mechanics of the cochlea.

The present method was able to generate an adequate fit to the BM data of Russell and Murugasu (1997). The AN data reported by Guinan and Stankovic (1996) showed considerable variation between the response of AN fibers to MOC stimulation. Nevertheless the model was able to simulate these changes without any special reference to the fiber type. Once the fiber had been modeled for the control condition, an appropriate response to efferent stimulation followed naturally.

The modified model is intended as a tool for the study of the contribution of efferent effects in the processing of complex sounds such as speech and particularly speech in a masking background. A similar model has already been implemented in the context of speech recognition by Ghitza et al. (2006). Their aim was to demonstrate enhanced representations of speech in background noise. The positive outcome of this evaluation offers support to his strategy. In this respect simulating the data of Dolan and Nuttall (1988) is particularly relevant. They showed that the CAP amplitude/level function for tones is reduced when studied in a fixed noise background. However, they also demonstrated that the rate/level function is partly restored when the MOC bundle is stimulated and confirmed the relevance of the efferent system to the unmasking of sounds in noisy backgrounds (Kawase et al., 1993). It is encouraging that the model can simulate both of these effects; the suppression by noise and the unmasking by MOC activity.

VII. CONCLUSIONS

(1) A simple attenuation of the basilar membrane response of the model is all that is required to reliably model the effect of stimulating the MOC system.
(2) The model can be used to demonstrate the unmasking of signals in masking background noise by (efferent) attenuation of the input.
(3) This makes this model a suitable platform on which we can further study the functional role of the MOC system in auditory perception.

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