A Silicon Representation of the Meddis Inner Hair Cell Model

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Abstract: The Meddis model is a widely accepted, but computationally intensive computer model of the mammalian inner hair cell. We have produced an analogue VLSI implementation of this model that operates in real time in the current-domain by using translinear and log-domain circuits. Our circuit is tested against the Meddis model for: (a) rate level functions for onset and steady state response; (b) recovery of spontaneous activity; and (c) low frequency synchronisation. The advantages of this circuit over other electronic inner hair cell models is its nearly exact implementation of the Meddis model which can be tuned to behave similarly to the biological inner hair cell. This has important implications on our ability to simulate the auditory system in real time. Furthermore, the technique of mapping a mathematical model of first-order differential equations onto an implementation with log-domain filters allows us to implement a host of models using the same approach.

Introduction

This paper offers an analogue VLSI representation of the Meddis model which is the most widely accepted computational model for the function of the inner hair cell [1]. Sound captured by the eardrum is translated into movement of the fluid in the cochlea, which in turn makes the basilar membrane in the cochlea vibrate (see Figure 1). This vibration is transduced into a neural signal by the inner hair cells and results in firing of the auditory nerve cells. To mimic this process past silicon cochleae [2],[3] have used non-linear low pass filters to produce the adaptation characteristic of the inner hair cell (IHC). These IHC circuits responded favourably to a simple set of stimuli, but failed with more complex stimuli [2].

In the design presented here we use log domain low pass filters to map the differential equations of the Meddis inner hair cell model to circuits on a silicon chip. This circuit preserves the flexibility of the Meddis model and is also in agreement with physiological data. The circuit implements an improved electronic model of the inner hair cell function which exhibits the correct time constants of adaptation over a large range of stimulus conditions.

The Meddis Model

Inner Hair Cells (IHC) are contained within the Organ of Corti which is located on top of the basilar membrane, inside the cochlea. The hair cells are the actual transducers that transfer the mechanical stimulus in the cochlea to the firing of auditory nerve cells.

IHC function is characterised in the Meddis model by describing the dynamics of neurotransmitter at the hair cell synapse (membrane-cleft boundary, see Figure 1). Transmitter is transferred between three reservoirs in a reuptake and re-synthesis process loop (see Figure 2).

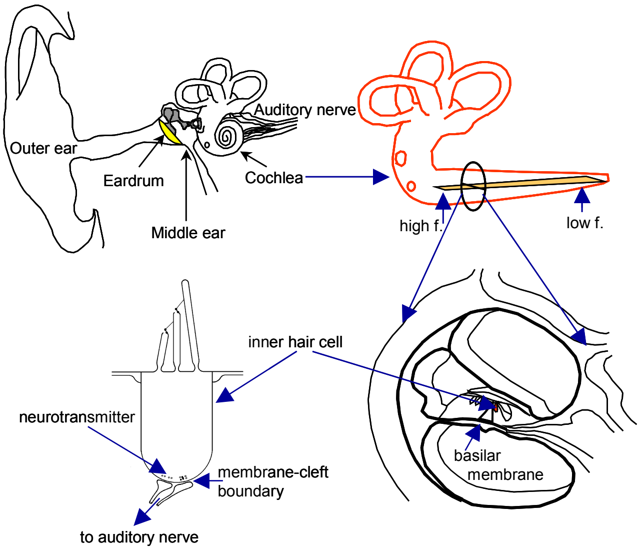

Figure 1: Human Ear and Inner Hair Cell

The first reservoir is a transmitter factory that releases neurotransmitter at the hair cell boundary and delivers it to the second reservoir, the free transmitter pool. The amount of neurotransmitter released from the pool into the cleft is controlled by changes in the permeability of the cell membrane. This fluctuates as a function of the intra-cellular voltage, which is directly related to the instantaneous mechanical stimulus amplitude. Some transmitter is lost in the cleft through diffusion and a further fraction taken back up into the cell. The remaining transmitter in the cleft stimulates the post-synaptic afferent fibre of an auditory nerve cell. The level of transmitter in the cleft dictates the probability of the nerve cell firing (spiking). Transmitter taken back up into the cell is initially reprocessed and stored in a third reservoir in preparation for delivery to the free transmitter pool. Incorporation of this third reservoir enables the model to display two-component adaptation typical of real inner hair cells.

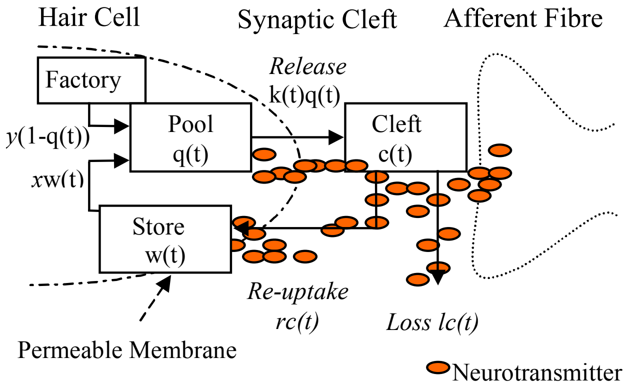

Figure 2: The Meddis Inner Hair Cell Model

The equations representing the Meddis Inner Hair Cell model are:

$$k(t) = \frac{g[s(t)+A]}{s(t)+A+B} \quad \text{for } s(t)+A>0 \qquad (1)$$

$$k(t) = 0 \qquad \text{for } s(t)+A \le 0$$

$$\frac{dq}{dt} = y[1-q(t)] + xw(t) - k(t)q(t) \qquad (2)$$

$$\frac{dc}{dt} = k(t)q(t) - lc(t) - rc(t) \qquad (3)$$

$$\frac{dw}{dt} = rc(t) - xw(t) \qquad (4)$$

$$prob(event) = hc(t)dt \qquad (5)$$

The permeability of the cell membrane is represented by *k(t)*. A, B, and g are constants of the model. In the absence of sound *k(t)* = *gA*/(*A*+*B*) which represents the spontaneous response of hair cells at rest.

The level of available transmitter in the pool, *q(t)* depends on the amount of transmitter manufactured, *y[1-q(t)]*, the amount reprocessed, *xw(t)*, and the amount lost to the cleft, *k(t)q(t)* (eq. 2). The cleft receives this amount, *k(t)q(t)*, where some transmitter is lost through diffusion, *lc(t)* and some actively returned to the reprocessing store, *rc(t)* (eq. 3). The reprocessing store receives transmitter at a rate, *r* and returns it to the free transmitter pool at a rate *x* (eq. 4).

The remaining level of transmitter in the cleft determines the probability of the afferent nerve firing. The constant, *h* is used to scale the output for comparison with empirical data.

Current Domain Description

The Meddis inner hair cell model was transferred to the current domain to allow the use of log domain filters whose operation is linear in the current domain.

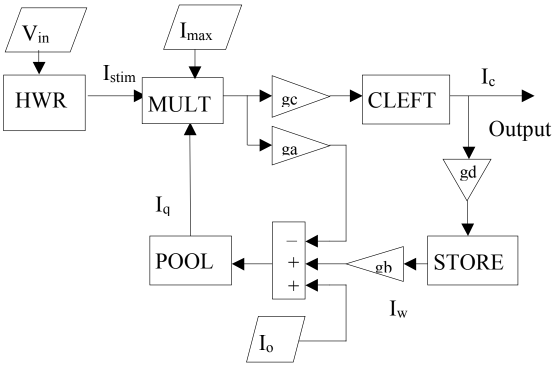

Figure 3: The Meddis Model in the Current Domain

Equation (1) of the Meddis model is represented by a half-wave rectification (HWR) function that exhibits the spontaneous bias of the inner hair cell. Rather than use a complex circuit to directly implement this function, it is approximated in the current domain using a differential pair with a shift to create a sigmoid function with a similar shape to equation (1).

$$hwr(V_{in}) \approx I_{stim} = \frac{I_{bias}}{1+e^{(V_{ref}-V_{in})/nU_T}} - I_{shift} \qquad (6)$$

where n is the slope factor of the MOS transistor and $U_T = \frac{kT}{q}$ is the thermal voltage.

The multiplication (MULT) of the permeability function *k(t)* with the available transmitter I_q and normalised by a constant I_{max} is represented by a current I_d. We can thus write:

$$I_d = I_q k(t) = \frac{g \times I_{stim}}{I_{max}} I_q \qquad (7)$$

The three differential equations (2), (3) and (4) are rewritten as difference equations, with each constant of the model represented by a time constant. The model was further simplified by replacing time constant ratios with dimensionless gains. This step makes the model easier to manipulate and time constants can now be changed without effecting the gains and vice versa.

$$(s\tau_y + 1)I_q = I_o - g_a \frac{I_{stim}}{I_{max}} I_q + g_b \times I_w \quad (8)$$

$$(s\tau_c + 1)I_c = g_c \frac{I_{stim}}{I_{max}} I_q \quad (9)$$

$$(s\tau_x + 1)I_w = g_d \times I_c \quad (10)$$

where:

$$g_a = \frac{\tau_y}{\tau_g}; g_b = \frac{\tau_y}{\tau_x}; g_c = \frac{\tau_c}{\tau_g}; g_d = \frac{\tau_x}{\tau_r} \quad (11)$$

and:

$$\tau_y = \frac{1}{y}; \tau_c = \frac{1}{l+r}; \tau_x = \frac{1}{x}; \tau_g = \frac{1}{g} \quad (12)$$

The Circuits

Log Domain Filters

Log domain circuits are dynamic translinear circuits formed by including a capacitor in the translinear loop [4]. The relationship between input and output current is linear, while the logarithmic (compressive) voltage-current relationship provides these filters with high dynamic range. We use a first order log domain filter, first investigated by Frey (1993) [5] implemented with MOS transistors operating in the weak inversion mode (Figure 4).

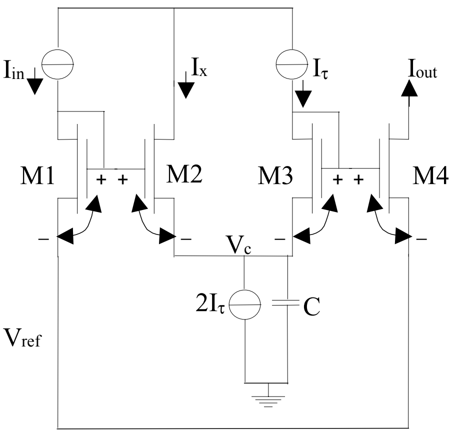

Figure 4: The Log-Domain Low Pass Filter

This circuit can be analysed using the translinear principle. The product of drain currents of transistors facing clockwise is equal to the product of drain current of transistors facing anti-clockwise[4]. For *M1, M2, M3* and *M4* this gives:

$$I_{out} I_x = I_{in} I_\tau \quad (13)$$

The summation of currents at node Vc yields:

$$I_{out}(C\frac{dVc}{dt} + 2I_\tau - I_\tau) = I_{in} I_\tau \quad (14)$$

As *M3* and *M4* form a current mirror their drain currents are related by (assuming *M3* and *M4* are matched and operating in weak inversion):

$$I_{out} = I_\tau e^{(V_c - V_{ref})/U_T} \quad (15)$$

Differentiating (15) gives:

$$\frac{dI_{out}}{dt} = \frac{I_{out}}{U_T}\frac{dV_c}{dt} \quad (16)$$

or:

$$\frac{dV_c}{dt} = \frac{U_T}{I_{out}}\frac{dI_{out}}{dt} \quad (17)$$

Substituting (17) into (14) then gives us:

$$I_{out}(\frac{CU_T}{I_{out}}\frac{dI_{out}}{dt} + I_\tau) = I_{in} I_\tau \quad (18)$$

or

$$\tau\frac{dI_{out}}{dt} = I_{in} - I_{out} \quad (19)$$

where $\tau = CU_T/I_\tau$. This circuit thus implements a low pass filter with a time constant determined by the value of the capacitor C, and tunable by the current I_τ.

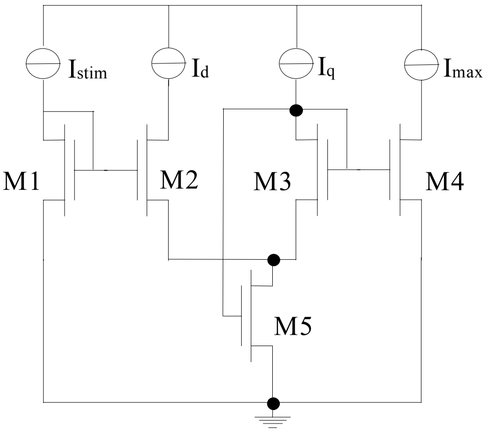

Figure 5: Translinear Multiplier

Translinear Multiplier

A translinear circuit that functions as a one-quadrant multiplier is used to generate the product of I_q and the permeability function (Figure 5).

$$I_d = I_q \times k(t) = \frac{gI_q \times I_{stim}}{I_{max}} \quad (7)$$

The inputs to the circuit are I_{stim}, I_q and I_{max} and the output is I_d. The transistors *M1, M2, M3* and *M4* form the translinear loop and *M5* is an adaptive bias transistor that actively biases *M2* and *M3*.

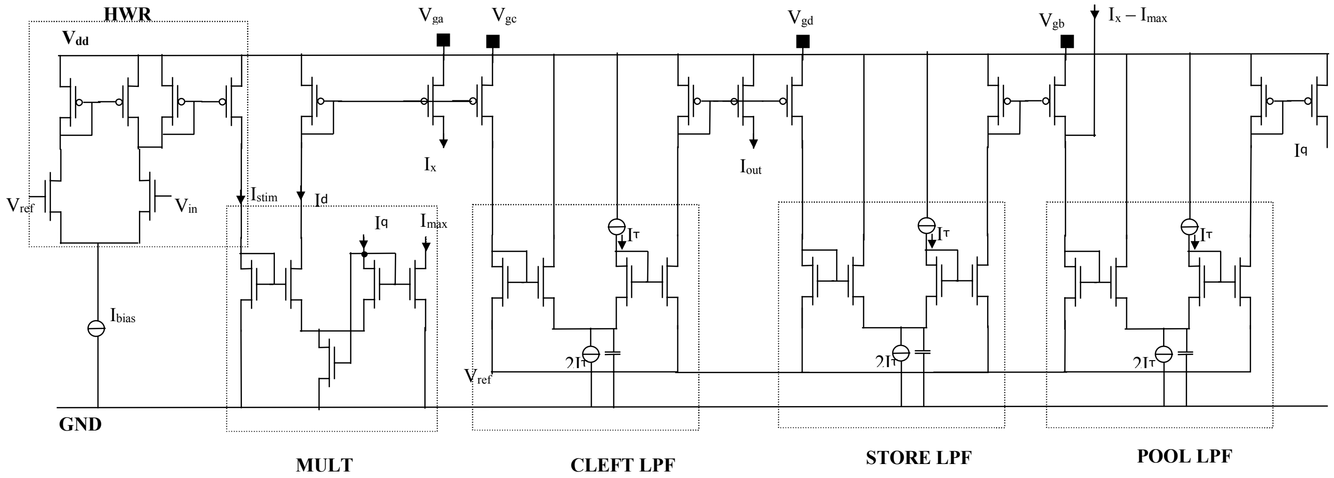

Figure 6: The IHC Circuit

The IHC Circuit

Three log domain low pass filters and the multiplier circuit are used to generate the IHC circuit of Figure 6. Variable gain current mirrors connect these stages to provide off chip control of the gains g_a, g_b, g_c, g_d.

The HWR circuit implements equation (6), providing conversion from voltage (output of a silicon cochlea) to current and half-wave rectification. The MULT circuit implements the generation of I_d, as in equation (7). The three low pass filters, CLEFT LPF, STORE LPF and POOL LPF implement equations (8), (9), and (10) respectively.

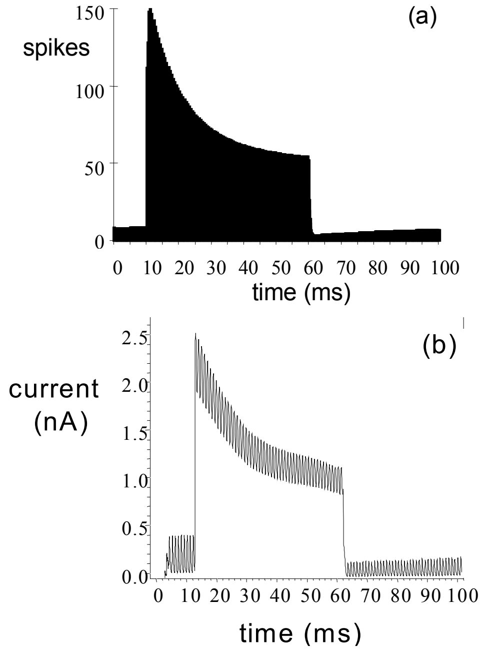

Figure 7: Comparison between (a) PSTH of the Meddis (1986) model [7], (b) SPICE simulations of the circuit.

Test Results

The circuit has been implemented in the AMI 1.2u process. Here we compare the response of the circuit to the response of the Meddis hair cell model to test the ability of the circuit to predict inner hair cell response. The Meddis hair cell model itself has been successfully compared to physiological data elsewhere [6]

The response of an inner hair cell model is shown by Meddis as a Post-stimulus time excitation histogram (PSTH). The response of the circuit to a tone burst compares well to a PSTH of the response predicted by Meddis' hair cell model (Figure 7).

The robustness of the circuit to variations in the parameters was investigated. The characteristic adaptation profile of the Meddis model was preserved for most parameter sets. However some combinations produced unstable results. Table 1 summarises the general effect of these parameters.

Time constants	Parameter Function
τ_y	Time constant of slower adaptation.
τ_x	Time constant of rapid adaptation.
τ_c	With little effect on adaptation, this filter is responsible for generating the low pass behaviour of the IHC response. See experiment (c).
Gains	
g_a	Increases effect of slow adaptation by limiting the amount of transmitter manufactured in the factory.
g_b	Decreases effect of rapid adaptation, by limiting the amount of transmitter re-uptaked through the store.
g_c	Controls the amplitude of the output. Same effect as g_b on adaptation.
g_d	Same effect as g_b on adaptation.

Table1: Model Parameters

Next, three tests of mammalian inner hair cell function, as used by Meddis [1], were used to verify the IHC circuit:

(a) Rate level functions for onset and steady state response.

These functions compare the response of onset rate and steady state rate to tone burst stimuli of varying amplitude. The onset rate is measured within the first 1ms and should increase with stimulus amplitude. The steady state rate is measured after 300ms and should remain constant across the measured stimulus range (Figure 8). The circuit shows the same behaviour, but there are some minor differences. These are mainly due to the fact that the HWR circuit is not an exact implementation of equation (6).

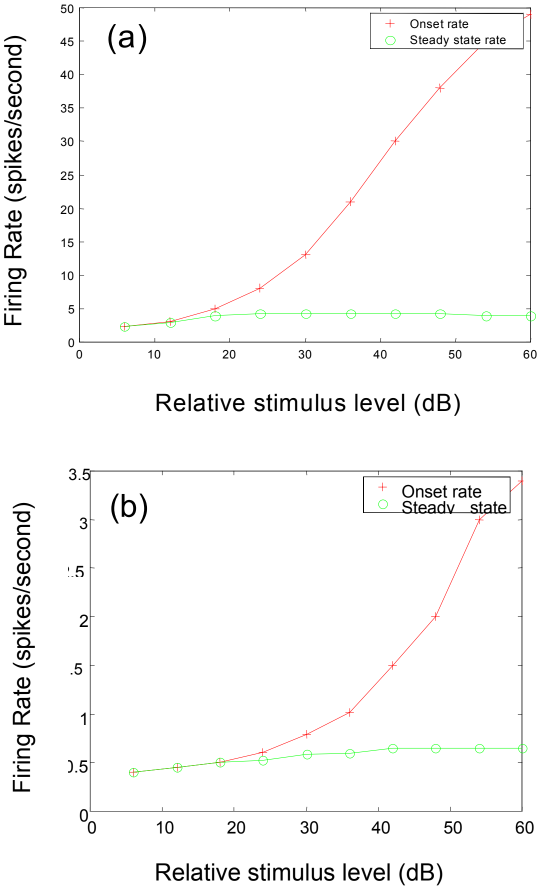

Figure 8: Rate Level Function (a) Meddis Inner Hair Cell Model, (b) SPICE simulations of the IHC circuit response.

(b) Recovery of spontaneous activity.

After a tone burst, the auditory nerve firing rate ceases briefly before recovering to the spontaneous rate. A single exponential with a time constant between 20 and 100ms describes the recovery function. Meddis reports a delay to recovery of 30.4ms. The circuit implementation displays a 56.6ms delay in returning to spontaneous rate. Although these delays differ, the delay predicted by the circuit is significantly closer to Meddis' model than any of the other seven models previously tested [1].

(c) Low Frequency Selectivity.

At low frequencies the auditory nerve responses synchronise or 'phase lock' with the stimulus tones to demonstrate a high magnitude A.C. response that resembles the stimulus signal's phase characteristics. At frequencies above 1kHz the A.C. component drops off and the phase information of the stimulus is lost. This is represented in the Meddis model by the store filter at 1kHz. The circuit shows a clear reduction in the A.C. component of the response at high frequency, in agreement with physiological data and the Meddis model [6] (Figure 9).

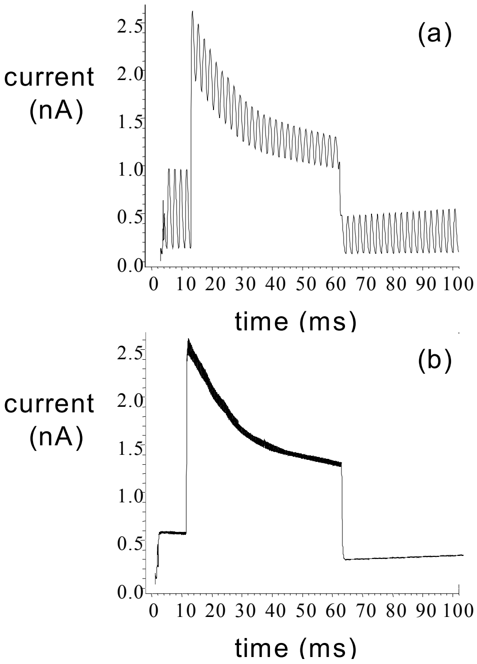

Figure 9: Low frequency synchronisation (a) Response at 500Hz; (b) Response at 5kHz.

Discussion

We have simulated the response of a chip containing two IHC circuits and a separate low pass filter circuit. The chip has been fabricated as a tiny-chip in the AMI 1.2µ process through MOSIS and is currently being tested.

This circuit successfully implements the Meddis model in silicon and compares favorably against three tests of hair cell function. The method of using log domain filters to directly map the system of differential equations to a circuit in the current domain is an example of the usefulness of translinear circuits. This method can be expanded to a general technique of circuit design for models consisting of first-order differential equations.

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