

A Holistic Model Of Human Touch *

Dianne Pawluk [†]

dianne@hrl.harvard.edu

TEL (617) 496-9098

Robert Howe

howe@das.harvard.edu

TEL (617)496-8359

Division of Applied Sciences

Harvard University

29 Oxford Street

Cambridge, MA 02138

To formulate a coherent explanation of the dynamic response of touch fibres (mechanoreceptors) to mechanical stimuli applied to the skin surface, we must develop a holistic model which includes all of the fundamental constituents. These constituents are: the mechanics of the skin, the mechanics of the end organ, the creation of a generator potential, the initiation of an action potential, and (for some units) the branching structure of the afferent fibres. We present preliminary results on the development of such a model. Our initial analysis will consider all but the last of these components.¹

1 Background

There are many sensors which respond to mechanical stimuli throughout the body. We will focus on the four primary types of mechanoreceptive units found in the nonhairy (glabrous) skin of the human hand, as they are the most important for exploration and manipulation. These receptors are classified in terms of speed of adaption, either 'Fast Adapting' (FA, no static response) or

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[†]First and corresponding author.

¹The effect of this last component is relatively unimportant for the initial experimental data, as the stimulus probe is a relatively flat indenter covering all branches of each afferent unit.

‘Slowly Adapting’ (SA, static response present), and by the size of their receptive fields, either type I (small, sharp borders) or type II (large, diffuse borders). Previous models of mechanoreception include: a static model of the skin mechanics [Phillips and Johnson, 81] and a dynamic model of the generator potential and impulse initiation [Freeman and Johnson, 81]. Our model additionally considers the end organ mechanics and the issue of consistency between these factors.

The models that we present are primarily based on the response of the different types of mechanoreceptors to sinusoidal displacement inputs experimentally obtained by Johansson, et al., [82]. The nerve impulses of individual afferent fibres were measured using microneurography in alert human subjects. The test stimuli were sinusoidal displacements applied perpendicular to the skin varying in amplitude (0.002 - 1.0 mm) and frequency (0.5 - 1024 hz). The measured frequency response for each receptor type is given in Figure 1. Note that the y-axis is in terms of nerve impulses per input frequency cycle and that 0 db corresponds to an amplitude of 1 mm.

2 Preliminary Models and Simulation Results

The models which we consider are one-dimensional, lumped parameter models which are based on both morphological plausibility and on the experimentally measured frequency response functions described above. Because of uncertainty about the contribution of the highly nonlinear neural impulse initiation component to the response characteristic of any mechanoreceptor model, very simple models were examined initially.

The first such model is shown in Figure 2a. It represents the skin, the end organ and the nerve membrane as simple springs, the generator potential as a simple proportionality to the nerve membrane displacement, and the conduction of the nerve fibre by the Hodgkin-Huxley equations [Hodgkin and Huxley, 52]. The input to the model is the displacement of the skin surface and the output is the time history of the nerve impulses initiated. Note that in this model the mechanical components contribute essentially nothing to the form of the output signal. This is because they form a simple proportionality factor which only affects the input range to which the model responds.

The model was simulated for a sinusoidal displacement input with varying amplitude (over the entire range which produced a nerve impulse train) and frequency (0.5 - 512 hz). The frequency response is shown in Figure 2b. The amplitude levels are presented in decibels, where 0 db corre-

sponds to the maximum input level; this non-dimensionalizes the input range and enables the model to be viewed independently of the proportionality constants. Note that the output is in terms of nerve impulses per input frequency cycle to facilitate the comparison with the experimental results in Figure 1.

The shape of the frequency response function (Figure 2b) is similar to those experimentally obtained for both SA type units: at large amplitudes the response is hyperbolic and at lower amplitudes it is an inverted U-shape. In addition, the variation of the response as a function of the input amplitude (not shown) is also similar, being logarithmic in both cases. The results also suggest that the shifting of the ‘peak’ of the frequency response with amplitude, most apparent in the responses of the FA type units, is an inherent property of the nerve membrane rather than due to nonlinearities in the skin mechanics.

However, there are two major discrepancies between this model and the SA type units: (1) the nerve impulse rate in the model is over an order of magnitude larger than the afferent units, and (2) the decibel input range to which the model responds is smaller than for all the receptors except the SAII units.

The addition of a simple mechanical high-pass filter (i.e., a single zero in the transfer function of the mechanical components) alleviates both of these discrepancies. In this second model (Figure 3a), the simple springs used to model the skin, end organ and nerve membrane are replaced with dampers, and the generator potential becomes proportional to the derivative of the nerve membrane displacement. This emphasizes the viscous properties of these viscoelastic materials. The model results in a derivative relationship between the displacement of the skin surface and the input current of the nerve fibre equations.

The model was simulated for sinusoidal displacement inputs of varying amplitude and frequency, as above for the ‘spring’ model. The frequency response is shown in Figure 3b. Both the magnitude of the nerve impulse rate and the decibel input range are comparable to the mechanoreceptive units. More specifically, the results are also similar to the FA type units in their general form and exhibition of ‘shifting peaks’ with amplitude.

The results from these two models suggest that modelling the mechanical components with carefully placed simple zeros and poles coupled with the Hodgkin-Huxley equations will explain the frequency responses of the mechanoreceptive units. A further aspect of the experimental re-

sults which is important to take into consideration is the phase of the input cycle to which the different types of mechanoreceptive units respond. Qualitatively, the SAI and SAII units respond principally to the indentation phase; the FAI units respond to both phases, but much less to the retraction phase; and the FAII units also respond to both phases, but more to the retraction phase [Johansson, et al., 82]. These experimental results can be compared to simulations of models using simple mechanical components, as above.

The simulation results showed that for a mechanical component consisting of: (1) a simple gain, the response occurs over the entire input cycle; (2) a simple derivative ($\frac{dx}{dt}$), the response occurs only on the indentation; and (3) a second derivative ($\frac{d^2x}{dt^2}$), the response occurs primarily on the retraction, but to some degree on the indentation. These results suggest that the SAI and SAII units can be modelled by first order systems, and the FAI and FAII units by second order systems (with the poles placed at much lower frequencies for the FAI units than for the FAII units).

3 Conclusions and Future Work

From the insight gained in examining these initial models, more appropriate models are proposed based on: (1) whether they can produce the desired overall shape of the responses, including phase characteristics, (2) the additional constraint that all units must share the same model of skin², and (3) morphological plausibility. The proposed models are given in Figure 4. Subsequent work will be directed at verifying these models.

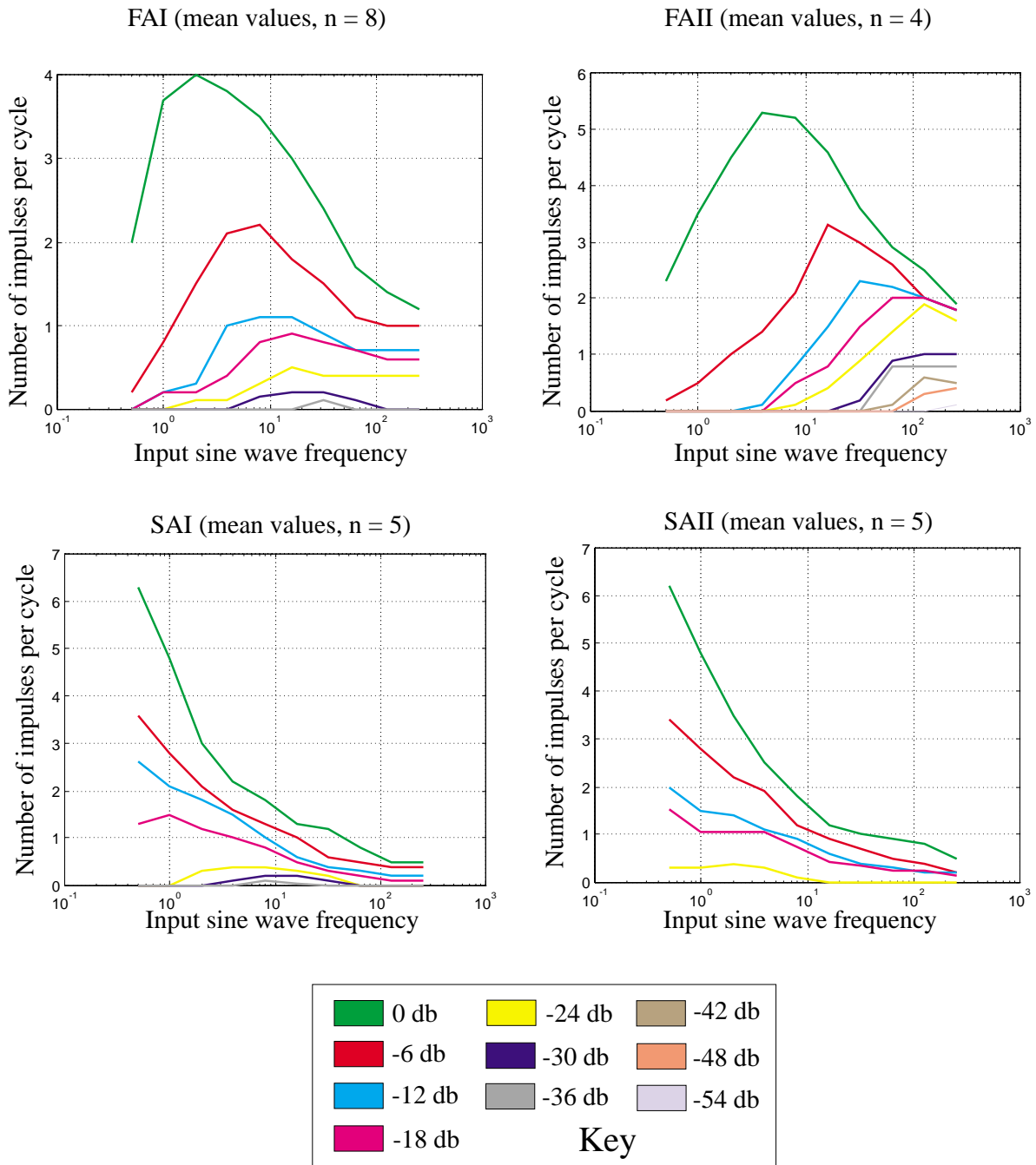
We have shown that the Hodgkin-Huxley equations coupled with simple mechanical components capture the essential properties of the experimental frequency responses. Based on these results, we have proposed more complex models to explain the responses of the four types of mechanoreceptors in the human hand. The simplicity of the models should facilitate further examination of mechanoreception, including models of branching afferent fibres and of population responses.

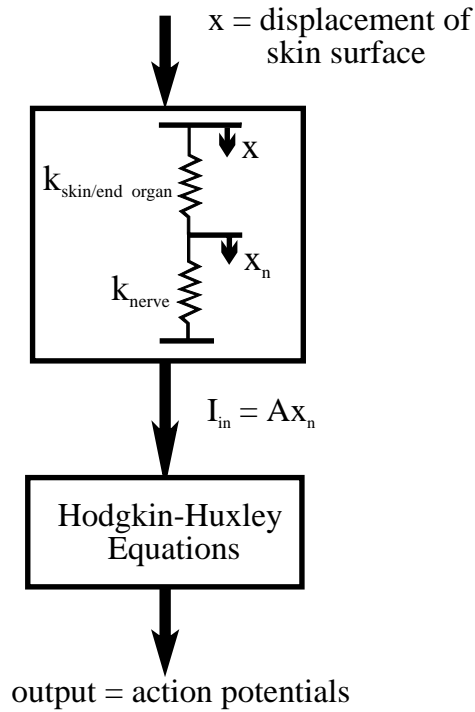
²Although the type I and type II units are at different depths, statistically there is very little variation due to this parameter in the experimental data used to develop the models.

References

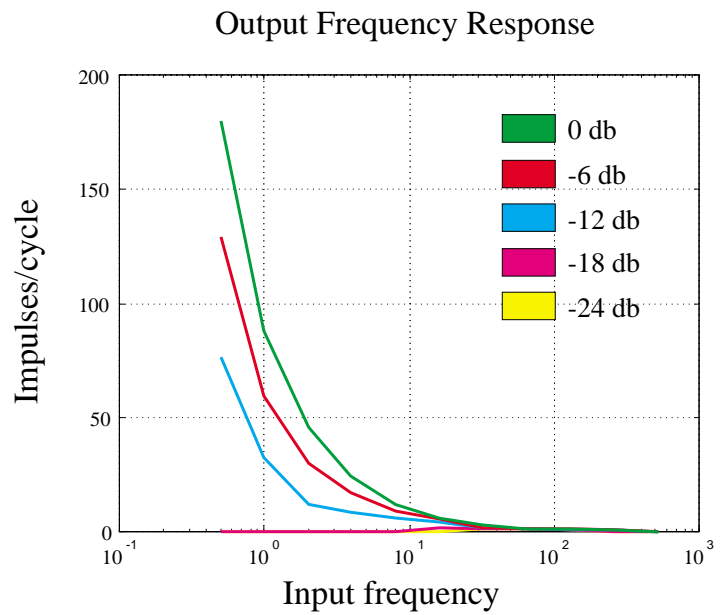
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Figure 1: Frequency Response Functions Of The Mechanoreceptors
(adapted from Johansson, Landstrom and Lunstrom, 1982)



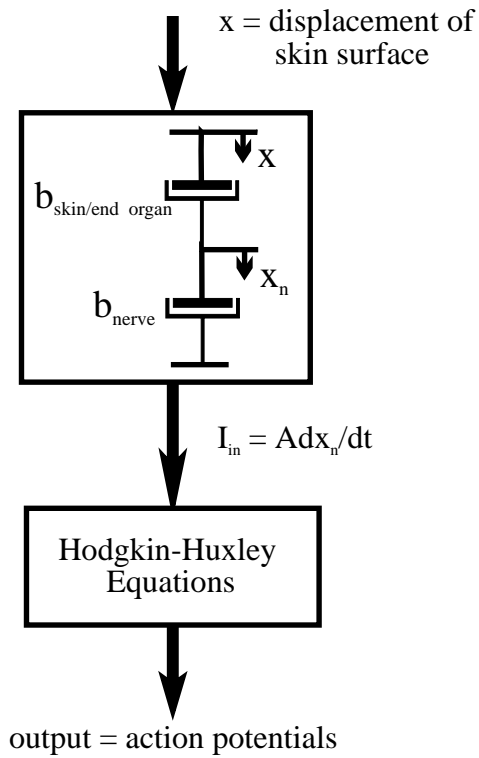


(a)

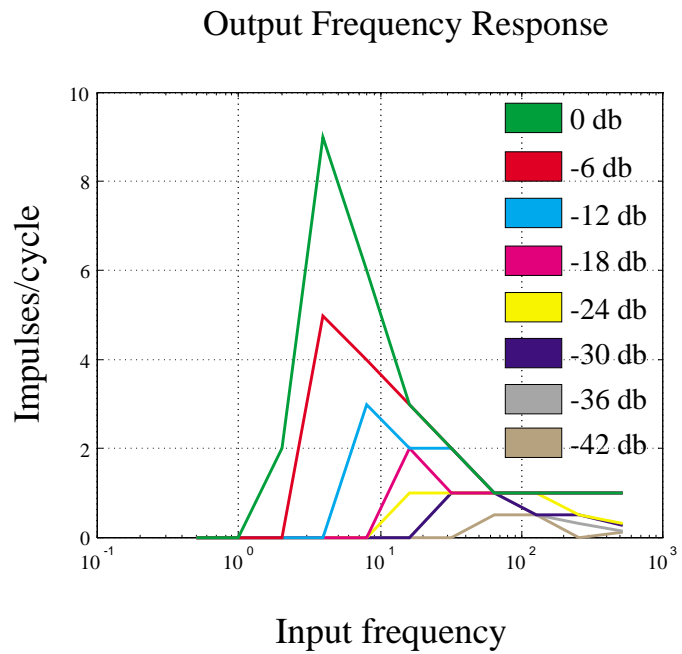


(b)

Figure 2. (a) Spring model of the skin, end organ and nerve membrane proportionally coupled to the Hodgkin-Huxley Equations, (b) Frequency response function of the ‘spring’ model shown above.



(a)



(b)

Figure 3. (a) Damper model of the skin, end organ and nerve membrane proportionally coupled to the Hodgkin-Huxley Equations. (b) Frequency response function of the ‘damper’ model shown above.

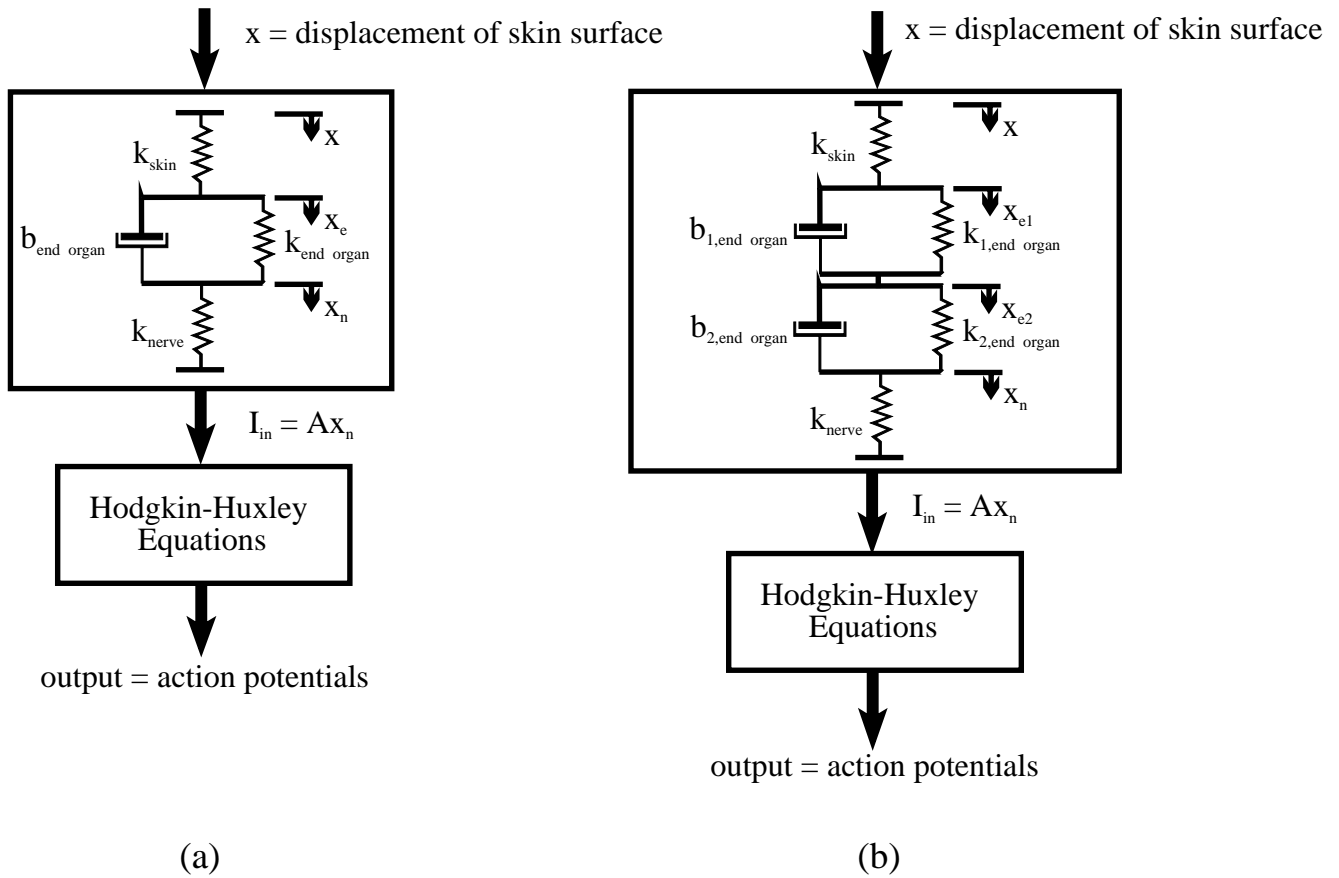


Figure 4. Proposed Models. (a) Model of the SAI and SAII units. (b) Model of the FAI and FAII units. Same parameters for the skin and nerve fibre for all models. Different parameters for the end organs of each of the four different types of mechanoreceptors.