Short-term adaptation in the auditory periphery: What is it and what is it good for?

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Short-term adaptation is a universal property of responses of single auditory nerve fibers and presumably arises in the synapse between hair cells and fibers. Adaptation obeys superposition and it can be modeled by a linear high-pass filter. Cochlear implants bypass this synapse, and when this filter is added to cochlear implant sound processors, implant performance improves for a variety of tasks.

As sensory scientists we have at our disposal a large array of measuring instruments and a wide variety of measures to quantitatively describe response parameters in the nervous system. Nevertheless the question invariably remains-how do we evaluate which aspects of what we measure physiologically are important to sensation and perception, i.e. which are used by the brain? Partial answers to this question involve correlating neurophysiological input output functions with psychophysical input-output functions. New previously unmeasured psychophysical input-output functions can also be predicted and tested based on the hypothesized relationships between physiology and psychophysics. Generally these kinds of tests can only be done for a limited number of situations. The development of sensory substitution devices, such as cochlear implants, provides an opportunity to advance this evaluation by modifying some of the characteristics of the transformations occurring in impaired sensory systems. The modifications will hopefully restore some of the performance of the impaired system and thus provide insight into the potential roles of the missing processing. This approach is made substantially more complicated by the reality that the brain is a "moving target" with its own "uncertainty principle". The brain can alter its modes of processing and develop new strategies in the face of altered processing.

The purpose of this brief review is to describe how a model of a presumably simple physiological phenomenon, auditory short-term adaptation, lead to a potential improvement in cochlear implant processing, which in turn sheds some light on a possible role of short term adaptation in hearing. In general, responses to onsets of sounds and changes in sound intensity are likely to play important roles in many aspects of hearing including for example detection, speech communication and source identification. This may be the reason that the auditory system has developed multiple mechanisms that emphasize changes in sound intensity at multiple levels of neurophysiological processing [1]. Short-term adaption observed in auditory-nerve responses to sound is one of the most peripheral examples of onset emphasis. It can be observed in its simplest form in the response to a constant-intensity tone burst where firing rate is maximum at response onset and decays to a steady-state value during the tone presentation [2]. Short-term adaptation with a time constant on the order of 40 ms is the subject of this paper, but there are also more rapid decays occurring within the first few milliseconds of stimulation and long-term effects extending over seconds. Firing rate drops below spontaneous rate immediately following tone offset, and the response to a probe tone is reduced.

When a tone burst is added to a longer background tone, the adaptation produced by the background tone can be observed, along with a reduction in firing to the short burst [3]. showed that this was an additive effect in that the increase in firing produced by the test tone was independent of the time delay from background onset to test-tone onset. When a short test tone is applied after a background or adapting tone the response to the test tone is also reduced [4]. showed that the aftereffect was subtractive, i.e. the reduction in firing rate was independent of the intensity of the test tone. Based on these additive and subtractive properties it was concluded that the adaptation process was fundamentally additive or linear in nature, i.e. it obeyed superposition.

Short-term adaptation is generally assumed to be absent in the receptor potentials of auditory inner hair cells [5,6] and in the response of auditory nerve fibers to electrical stimulation, at least at high current intensities [7]. It has been seen in post-synaptic potentials in some auditory nerve systems [6] and is generally attributed to the hair cell to auditory-nerve fiber synapse [8].

Some of the features of short-term adaptation described above led [3] to propose a three-stage model to describe adaptation as observed in single auditory-nerve fibers and it's interaction with input intensity (Figure 1).

The first stage consists of a time invariant saturating nonlinearity, presumably representing the transformation from sound intensity to inner hair-cell receptor potential. This is followed by an adaptation stage which is modeled by a linear, first order, high pass filter in order to account for the additive and subtractive effects of adaptation. This filter is responsible for the decay in response following the onset response to a constant -intensity input, as well as the reduction in response at the offset of the input (A negative, sub-threshold after effect of stimulation must also be assumed). The third stage was necessary to take into account the saturation in firing rate, at high neural firing rates, presumably due to neural refractoriness.

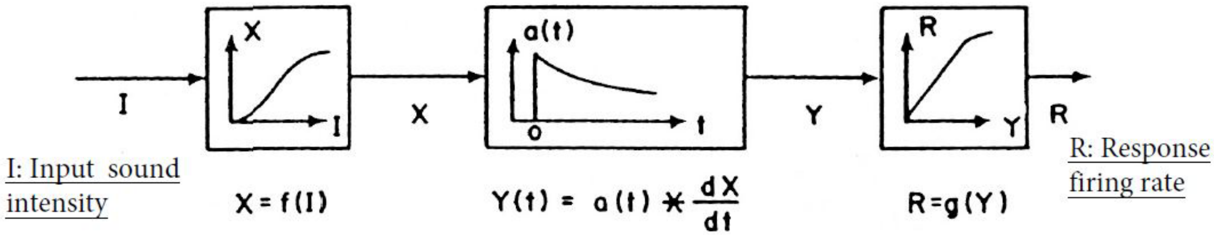

Figure 1: *The short term adaptation observed in auditory-nerve responses can be modeled by a "linear" filter with a response to a step input of* $A+Be^{-t/\tau}$ *sandwiched between two time invariant nonlinearities (adapted from Smith and Zwislocki, 1975).*

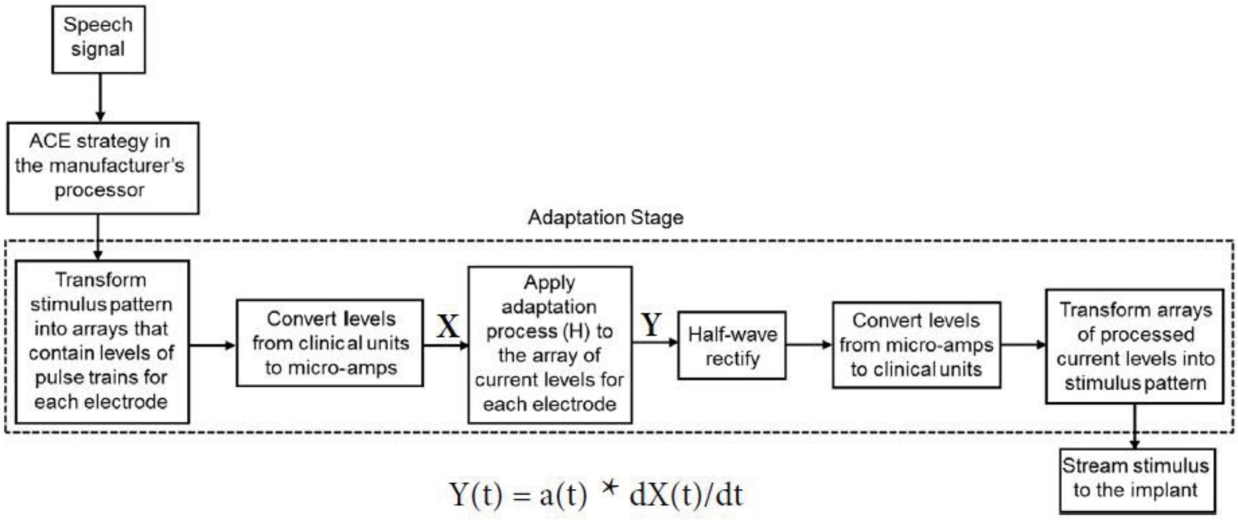

Figure 2: *A linear "adaptation filter" (H) can be inserted into each electrode channel of a cochlear-input speech processor to produce short-term adaptation and improve speech intelligibility (adapted from Azadpour and Smith, 2016).*

This oversimplified block diagram approach to adaptation was able to account for many of the effects of intensity and time on neural firing rates [3,4] and hence can be considered to be a reasonable first order description of the transformation from sound intensity to firing rate occurring in the normal auditory periphery. Various refinements to the basic block diagram model have occurred over time [9,10] in order to encompass additional details of the input-output transformations and to create more physiologically realizable components. In contrast to acoustic stimulation, when the auditory nerve is stimulated directly with electrical current, as in a cochlear implant, the transformation from hair cell to postsynaptic potential is bypassed, and hence the short-term adaptation that is produced in this transformation is absent [11]. Consequently to the extent that short-term adaptation is important in sound and speech perception, the effectiveness of the cochlear implant is potentially reduced. On the other hand adding short-term adaptation to cochlear implant processing creates an opportunity to improve cochlear implant performance and to evaluate short-term adaptation's potential importance in hearing. The basic model described above provided an opportunity to add "realistic" short-term adaptation to cochlear implant encoding in a laboratory setting [12,14]. Hence in a recent series of experiments [1] describe how a simplified model of peripheral short-term adaptation, based on the above neurophysiological results, can be added to cochlear implant speech processing (Figure 2).

In these experiments short-term adaptation was added to individual channels of simulated cochlear implant processors and a variety of speech related tasks performed by subjects who had been using their clinical implants for at least six months [15]. The parameters of the adaptation were optimized for best performance for a given subject and consisted of the time constant and amount of adaptation. This procedure resulted in improvements in various aspects of speech communication in their laboratory conditions. Consonant identification and sentence recognition in quiet had average improvements of 6% and 8% respectively.

Consonant recognition in babble noise also improved when adaptation was added. Information transfer improved for manner and place of articulation, but not for voicing. A more detailed description of the techniques, implementation and results are found in [16-18] It remains to be determined how to optimize the parameters of adaptation in cochlear implant channels, and whether it can produce every day improvements in cochlear implant hearing when utilized in the real world [19].

However, the results to date suggest that adding adaptation improves performance and optimizing the parameters has the potential of leading to further advances in cochlear implant hearing [10].

The developments outlined above show how physiological studies can lead to candidate improvements in electronic hearing, and experiments in electronic hearing can provide evidence as to the functional significance of the physiological findings [20,21]. Key components of this approach are physiological input-output measurements, utilization of quantitative models to account for the results, synthesis of the models to apply them to sensory substitution devices, and fine tuning the models to individual subjects with a goal of improving psychophysical performance.

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