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Review Article

Sensory Transduction: A Common Blue Print

Peter B Detwiler Ph.D.*

Department Physiology & Biophysics, School of Medicine, University of Washington, USA

***Corresponding author:** Peter B. Detwiler, Ph.D., Department Physiology & Biophysics, School of Medicine, University of Washington, Seattle, WA 98195 USA. Tel: 1 (206) 543-0957; Email: detwiler@uw.edu

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Abstract

Sensory receptors are transducers that convert a physical signal in the outside world into a cellular signal that can be integrated, transmitted, processed and interpreted by the nervous system. While the assortment of different types of sensory receptor is able to detect and selectively respond to a wide range of diverse extracellular signals they all work in basically the same way according to common blue print. They are compartmentalized input-output cells. For a specific signal to be detected it must first act on specialized membrane proteins (detector proteins) in the input or transduction region of the cell. This interaction generates a change in membrane voltage (receptor potential) by opening or closing ion channels either directly or indirectly via an enzyme cascade that controls the concentration of an intracellular second messenger (a cyclic nucleotide or calcium). The resulting electrical signal is communicated to the output region of the cell where it regulates Ca^{2+} dependent exocytosis of a chemical transmitter that carries the sensory signal to the next cell in the sensory pathway. These are the basic steps that underlie the operation of all sensory receptors. While the identity of the individual components will vary from one receptor type to another, the general blue print by which they function remains the same.

Introduction

Our goal here is to cover the basic features of sensory receptors to gain a general understanding of how they work. Why should we care how they work? Imagine you were born without any of your senses, no sight, hearing, smell, taste, touch, no sense of balance, gravity, hot, nor cold; no sensory input what so ever, nothing, and you were kept alive by whatever means necessary for 21 years at which time the question is would you have a thought in your head? If so what could it possibly be about, where could it have come from, what could have provoked it? This is a famous question first posed by David Hume, an 18th century Scottish philosopher, who used it to support the empirical conclusion that everything we know including our concept of self is derived from our sensory receptors [1]. If this is not enough to arouse an interest in how sensory receptors work, consider what your sex life would be like without them.

Sensory receptors are classic input / output devices

The input is a signal from the outside world, where the outside world includes both the external world that we live in as well as the internal world that the cells we are made of live in. While our sensory receptors can selectively detect tens of thousands of different external and internal signals there are only four different types or modalities of stimuli: chemical (chemoreceptors), mechanical (mechanoreceptors), light (photoreceptors) and temperature (thermoreceptors). The output of the sensory receptor is a chemical transmitter that is released by Ca^{2+} dependent exocytosis of transmitter containing vesicles using the same sequence of events that control the release of neurotransmitter at a synapse.

Sensory receptors are polarized cells with spatially segregated input and output compartments. The input or transduction compartment communicates with the output or synaptic terminal of the receptor cell via a change in membrane potential, a receptor potential that is generated by an increase or decrease in current flow into the cell through an ion channel (Figure 1). So, to understand how sensory receptors work we need to understand how the input signal operates (gates) an ion channel.

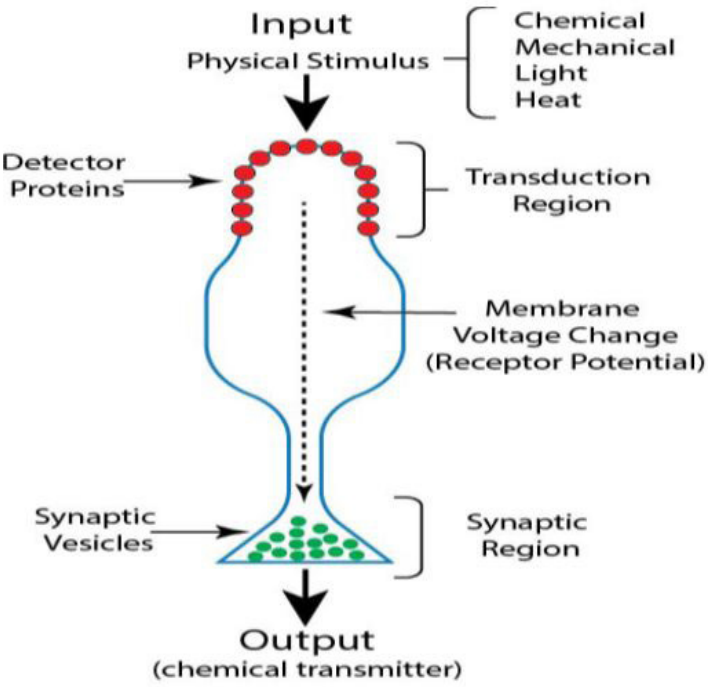

Figure 1: Sensory Receptors are compartmentalized input / output cells. The input is a physical stimulus that is detected by specialized membrane proteins in the transduction region of the cell. This generates a receptor potential (see Figure 2) that is communicated to the synaptic region where it triggers a change in the output (synaptic release) of a chemical transmitter (see Figure 3).

The surface membrane of the input compartment is populated by membrane proteins, which we will refer to as detector proteins. They are designed in such a way that the protein undergoes a conformation change when it receives a specific signal. This could be the binding of a ligand in the case of some, but not all, chemoreceptors, the application of a mechanical force (tension, shear, pressure, torque) in the case mechanoreceptors, electromagnetic radiation in the case of photoreceptors and heat in the case of thermoreceptors. The conformational change that is triggered by arrival of the sensory signal either directly gates (opens or closes) an ion channel that is an integral part of the detector protein, making the detector a receptor ion channel complex, or the conformational change activates a detector protein that is G Protein Coupled Receptor (GPRC), which in turn excites a G protein coupled enzyme cascade that ultimately gates an ion channel via change in the concentration of an intracellular second messenger, typically a cyclic nucleotide (cGMP of cAMP) or Ca^{2+} (Figure 2). In all known cases the ion channel that is controlled by the detector protein is a non-selective cation channel with a reversal potential typically near 0 mV. This results in a receptor potential that is either depolarizing (stimulus opens channel) or hyperpolarizing (stimulus closes channel). In all but two types of sensory receptors the transduction process generates a depolarizing receptor potential. The two exceptions, in which the receptor potential is hyperpolarizing are vertebrate photoreceptors, where the light activation of visual pigment (a GPRC) stimulates the hydrolysis of cGMP causing a cyclic nucleotide-gated cation channel in the surface membrane to close and certain types mechanoreceptors in which a decrease in force can cause the closure of mechanosensitive cation channels that are open under resting conditions.

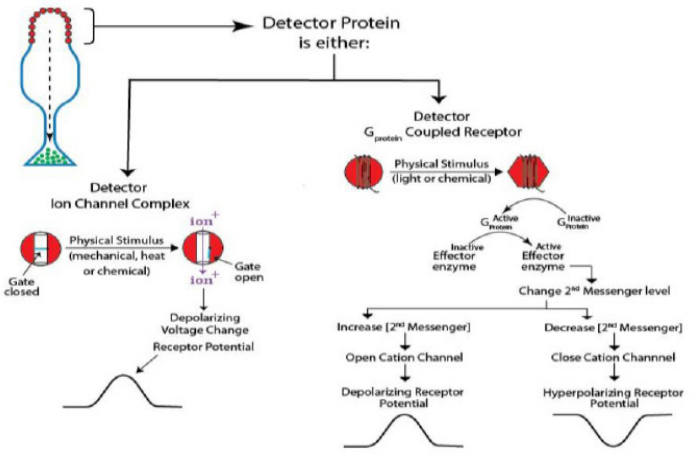

Figure 2: The transduction of a physical stimulus into an electrical signal is mediated by detector proteins that are either a detector ion channel complex or a G Protein Coupled Receptor (GPRC). Ion channels that are an integral part of the detector protein complex are cation selective and gated directly by the direct action of the physical stimuli they are designed to detect, which could be force, in case of mechanoreceptors, ligand binding, in the case of some types of chemoreceptors or heat, in the case of thermoreceptors. Detector proteins that are G Protein Coupled Receptors (GPRCs) are activated by either light, in the case of photoreceptors, of ligand binding in the case olfaction, some types of taste receptors and signal molecules used for cell-to-cell communication. The activated GPRC turns on a G protein coupled enzyme cascade that changes the level of an intracellular second messenger that gates a cation selective ion channel producing either a depolarizing or hyperpolarizing receptor potential depending on whether the second messenger level increased or decreased.

Sensory receptors that use a detector protein ion channel complex to convert a physical stimulus into an electrical signal include many kinds of chemoreceptors, taste receptors for salts and acids, all types of mechanoreceptors and thermoreceptors [2-14]. Stimuli that are transduced by GPRC detector proteins include photoreceptors, olfactory receptors, taste receptors for sweet, bitter and umami tastants and a host of receptors for signaling molecules used in cell-to-cell communication, such as hormones [15-18].

The receptor potential is a local voltage change generated in the transduction region of the receptor with an amplitude that depends on the strength of the sensory stimulus, i.e. the number

of detector proteins affected by the stimulus and thus the number of gated ion channels. The local receptor potential reaches the synaptic region of receptor cell via either passive spread or a conducted action potential depending on the distance between the input and output regions of the cell (Figure 3). Local voltage changes get smaller and slower as they spread passively from their site of generation, a consequence of what is commonly referred to as the cable properties of the cell [19]. If the receptor cell is compact and the distance separating the transduction and synaptic regions is short the decrement of the receptor potential is small and does not interfere with the transfer of information from the input to the output regions of the cell. These receptors are commonly referred to as primary sensory receptors (they do not generate action potentials) examples, include retinal rods and cones, auditory and vestibular hair cells and taste receptor cells. If the distance between the transduction and synaptic regions of the cell is too large for effective communication via passive spread, as in the case of olfactory receptors as well as cutaneous touch and temperature receptors, the expression of voltage gated Na+ channels in the intervening axon region of the cell support the generation of action potentials allowing the sensory information contained in a depolarizing receptor potential to be conducted to the synaptic terminal via a single or train of action potentials depending on the amplitude of the receptor potential (Figure 3).

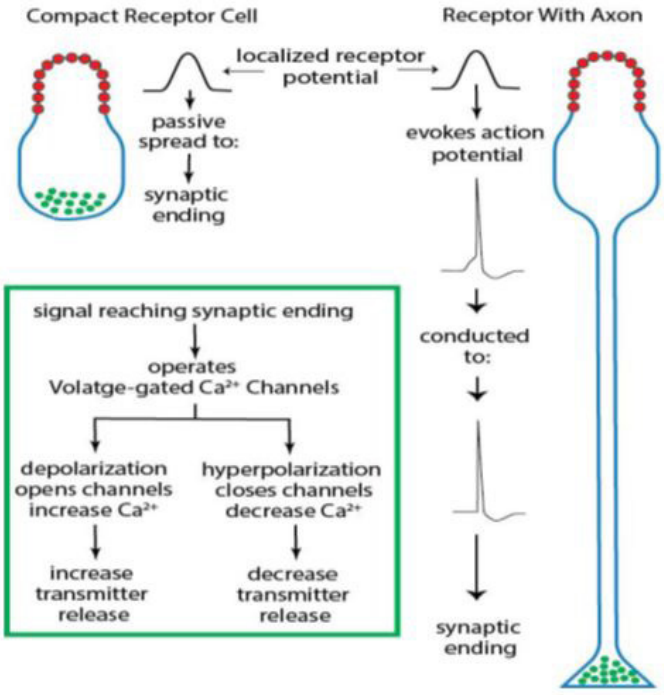

Figure 3: Receptor potentials reach the synaptic region of sensory receptors cell either by passive spread in compact cells without an axon or by triggering a propagated action potential in receptors that express voltage gated Na+ channels and have an axon. In both cases the electrical signal that reaches the synaptic region of the cell influences voltage-gated Ca^{2+} channels to either increase (if sensory signal is depolarizing) or decrease (if sensory signal is hyperpolarizing) Ca^{2+}-dependent exocytosis of chemical transmitter.

Conclusion

Sensory receptors generate an electrical signal in response to a diverse assortment of stimuli delivered in the form of either chemical, mechanical, radiant (light) or heat energy. In all cases they couple sensory input to synaptic output via a similar sequence of events (a common blue print) that follows a course based on three defining characteristics: 1. detector protein is either an ion channel complex or GRPC. 2. Receptor potential either depolarizing (the most common case) or hyperpolarizing. 3. Input (transduction) region of the cell communicates with the output (synaptic) region of cell via either passive electrical spread (primary sensory receptors) or conducted action potentials.

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