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Hypothesis

Sensory Spine-Necks may be Perceptible

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Abstract

Hypothesis: A sensation (e.g., the twinkle of a star in a night sky) arises in the opening of the spine-neck membrane of primary cortical sensory pyramidal neurons.

Introduction

Beginning in the 1950's, Barlow and others established that sensory neurons are responsible for sensations [1-9]. Mountcastle confirmed that sensory thresholds were similar in humans and other primates [10]. Libet, in his "time-on" studies, compared the duration of the neural activity and onset of "liminal" sensations [11]. He showed that sensations persist unfaded for 500 to 5000 ms, and that the threshold for sensory duration is approximately 200 ms [12].

A well-studied visual sensation is a phosphene. A phosphene appears as a flash of light. They can be elicited in all visual fields, demonstrate a precise location at a narrow visual angle of less than one degree, and discrete colors [13-17]. With a stimulus duration of 250 ms, the subject sees the same shapes each time, and different subjects see different shapes [36]. Phosphenes appear and disappear immediately when stimulation is turned on and off with tightly defined onset and duration [18-22].

Sensations Arise in Sensory Neurons in cortex.

Phosphenes can be elicited in mid-layer cortex pyramidal neurons by a single electrode spreading current less than 0.5 mm, capable of influencing as few as 50 cells. The sensory neuron and its cortical column are connected widely through brain and brainstem, but reproducible phosphenes require local activation [23 -37].

Cortical Sensory Neurons Respond in an "instant" (< 50 ms).

In cats, visual cortex neurons respond in approximately 35 ms, slightly faster for changes in luminance than contrast [38]. In rodents, the somatosensory cortex neurons respond to whisker deflection in 12 ms. The timing and duration of each step from external sensory receptor to the lick response at 317 ms has been studied by Carl Petersen's team [39; 40]. A single whisker deflection activated a single neuron in a cortical column that contains the neuron's soma, axon and complete dendritic arbor. Using voltage-sensitive dye imaging through a craniotomy window they showed that the excitation to a single stimulus was initiated in the column at 2 ms. GABA inhibition had no effect on this early response [41]. On the other hand, NMDA receptor-dependent plasticity was induced within two minutes, supporting a role for spine necks in memory [42]. Direct cortical stimulation was achieved via

juxta-cellular pipette voltage stimulation and was optimized with a stimulus duration of 200 ms [43-45].

Sensations last longer than an instant, they last

for a "moment" (50-400 ms).

The Petersen team also identified a late and prolonged depolarization at 50-400 ms. This "late" depolarization occurred in trained animals only. Whisker deflections stimulated action potentials in the same and nearby cortical columns in the first 50 ms followed by a rapid decline to baseline in 200 ms. The late potential, on the other hand, started at 50 ms and was sustained for 400 ms. The authors proposed that the late component causally participates in the subjective "sensory percept" [46 -45].

Cortical sensory spine-necks respond for a "moment" (50-200 ms).

Unique outpouchings along the sensory dendrite called spines receive the axons from the thalamus (Fig. 1).

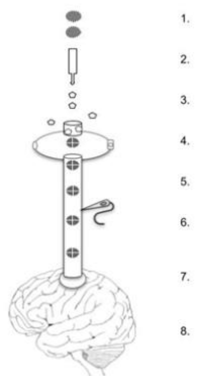

Figure.1.Peripheral Stimuli; 2. Thalamic Relay; 3. Glutamate; 4. Receptor. channels; 5. Positive ion influx; 6. Spine-neck EPSP with Electrode; 7. Dendrite; 8. Interneurons

In response to glutamate binding, the AMPA channel opens to positive ions initiating the depolarization along the membrane towards the dendrite. Nevertheless, the spine-neck potential does not significantly contribute to its own axon, leading to the proposal that spine-neck potentials are acting, not in the service of firing rates, but as an antenna system [29]. The spine neck's length, diameter and shape are actively controlled by the actin skeleton that increases electrical resistance in the spine-neck membrane [47, 48, 49, 50, 51, 52]. The spine-neck resistance prolongs the membrane potential to 50-200 ms, longer with continuing external stimulation [53, 54, 55, 56, 45, 57]. The spine-neck and axon share the same membrane, but the spine-neck potential lasts dramatically longer [6, 5].

Sensations may arise in cortical sensory spinenecks

Sensory spine-neck membrane potentials have precise spatial and temporal coordinates. One or a few may create a phosphene or may correlate with the smallest sensations. The adjacent NMDA receptors may save spine-neck potential patterns as memories. In the present moment the external environment is experienced by the individual during the same moment that the extracellular environment is open for (positive) ions entering the cell.

Phosphenes are sensations

Phosphenes are flashes of light evoked by stimulating the visual system mechanically or electrically. Phosphenes are typically small (less than 0.5 degrees of visual angle), round or complex patterns, and a variety of colors. They can be elicited in central and peripheral vision [13, 16, 58, 15, 17]. When a phosphene-eliciting stimulation duration of 250 ms is repeated, the subject sees the same shapes each time, different subjects see different shapes [18]. Phosphenes appear and disappear immediately when stimulation is turned on and off [19, 20, 30, 21, 23].

Phosphenes arise in primary visual cortex (V1) pyramidal neurons

Phosphenes can be elicited in primary visual cortex mid-layer pyramidal neurons by a single electrode spreading current less than 0.5mm [58, 36, 37,38,39, 40, 59,41, 42,43, 44,45]. In a mm2 of the human visual cortex there are 200,000 neurons and 3,084 billion (x109) synapses [60]. The search for a psychophysical mechanism has been focused on the fast-firing neural circuitry not the slow subcellular membrane potentials [46, 47, 49].

Synaptic spines on V1 dendrites have long, high resistance neck membranes

The V1 pyramidal neurons receive synaptic connections via the thalamus from the retina onto the dendritic spines. The postsynaptic membrane holds the AMPA- and NMDA- receptors for the primary excitatory transmitter (glutamate). The NMDA receptors modulate recall of those spine- necks [61].

The spine neck's length, diameter and shape are controlled by the actin skeleton molecules that dramatically increase electrical resistance in that section of membrane [62, 47, 48, 49,51, 52].

Spine neck membrane depolarizations are prolonged to 20-200 ms

From the synapse, the membrane depolarization spreads into the spine neck. The high electrical resistance in the spine neck prolongs the membrane potential from a few milliseconds to 20 to 200 milliseconds and longer with continuing external stimulation (53, 54, 55, 56, 45, 57).

Sensory membranes 'late component'

Since Barlow's studies in the 1950's, it is well-established that sensory membranes areresponsible for subjective sensations [1, 8, 2, 3, 7, 9]. Sensory thresholds are the same for humans and macaques [10]. Activity of specific peripheral receptors gives rise to specific elementary sensations [4]. Libet found that the sensory threshold was about 200 ms and that sensation persisted unfaded from about 50 ms to 5000 ms [12]. In his "Time-On" studies, he experimentally determined the correlation between the liminal sensation and the duration of neural activity [11]. Petersen and his colleagues have demonstrated that in response to whisker stimulation, mouse cortex barrel neurons respond with a "late component" that occurs 40-500 ms after stimulation; they propose that this late component causally participates in the subjective sensory percept [57, 58].

Hypothesis:

V1 spine-neck membrane potential durations of 50-200 ms will correlate with visual stimulation and subject self-report. Visual cortex spine-neck membrane potentials are perceptible because they linger beyond the threshold for detection of about 50 ms. When the sensory membrane remains polarized for more than 50 ms, a sensation is experienced in that present moment. External stimulation provides the sufficient succession of synaptic EPSPs to sustain the spine-neck in a prolonged depolarization. In lay terms, when you see the smallest twinkling star, one spine-neck in your is responding. When you see more, many spine-necks are responding. The spine-necks respond not just for an instant but for a 'split second' (200-300 ms), the flap of a bird's wing, and until the external stimuli change and the constellation of spine-necks change. Some such constellations we remember.

Contribution to the field

Dendritic spine-neck EPSPs are extraordinarily long in duration and unexplained. The spine-neck theory proposes that when the primary sensory neuron membrane at the spine neck is depolarized for an sustained duration, it is perceptible

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