

Importance of spike timing in touch: an analogy with hearing?

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Touch is often conceived as a spatial sense akin to vision. However, touch also involves the transduction and processing of signals that vary rapidly over time, inviting comparisons with hearing. In both sensory systems, first order afferents produce spiking responses that are temporally precise and the timing of their responses carries stimulus information. The precision and informativeness of spike timing in the two systems invites the possibility that both implement similar mechanisms to extract behaviorally relevant information from these precisely timed responses. Here, we explore the putative roles of spike timing in touch and hearing and discuss common mechanisms that may be involved in processing temporal spiking patterns.

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Introduction

Touch has traditionally been conceived as a spatial sense, drawing compelling analogies to vision. Indeed, both modalities involve a two-dimensional sensory sheet tiled with receptors (the retina and the skin) that each respond to local stimulation (radiant or mechanical). In both modalities, the spatial configuration of the stimulus is reflected in the spatial pattern of activation across the receptor sheet. In both modalities, higher order stimulus representations — of object shape and motion — are remarkably analogous [1–4]. The similarity between tactile and visual representations has been used as powerful evidence for the existence of canonical computations: the nervous system seems to implement similar computations to extract similar information about the environment, regardless of the source of this information [5].

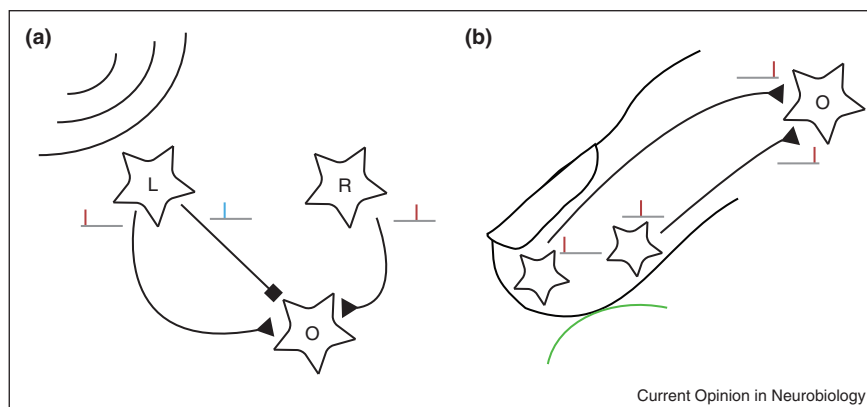
As compelling as the visual analogy is, however, there are aspects of touch that flout it, in particular its temporal precision and the putative functional role thereof. Indeed, cutaneous mechanoreceptive afferents respond to skin stimulation with sub-millisecond precision, and the relative latencies of the spikes evoked across afferents are highly informative about contact events [6**]. Furthermore, afferents respond to skin vibrations up to about 1000 Hz in a precisely phase-locked manner. Their responses to sinusoids, for example, are restricted to a small fraction of each stimulus cycle over the range of tangible frequencies [7,8,9*,10**,11]. This temporal patterning underlies our ability to distinguish the frequency of skin vibrations and even to discern fine surface texture. At a first approximation, these aspects of touch are more similar to hearing than they are to vision.

In the present essay, we examine the role of spike timing in the processing of tactile stimuli and draw analogies to hearing. Hearing, like touch, involves a highly temporally precise stimulus representation at the periphery: relative spike latencies across cochleae play a role in sound localization and the phase locking of auditory afferents contributes to pitch and timbre perception. First, we discuss potential analogies between the use of delay lines and coincidence detectors for auditory localization and for the tactile coding of contact events. Second, we explore parallels in the way the somatosensory and auditory systems extract information about the frequency composition of skin vibrations and sound waves, respectively.

Computing from differences in spike latency

One of the most remarkable examples of the role of spike timing in extracting information about the environment is in sound localization. Indeed, the relative time at which an acoustic stimulus reaches the two ears depends on the azimuthal location of the source. The small temporal disparities in the relative arrival of the stimulus at each eardrum — measured in the tens to hundreds of *microseconds* — are exploited to compute its azimuth using precisely timed excitatory and inhibitory interactions (in mammals) [12]. Specifically, neurons in the medial superior olive receive excitatory input from both cochleae, and strong and precisely timed inhibitory input from the contralateral one. As the relative timing of all excitatory and inhibitory inputs depends on azimuth, so does the strength of the response, which confers to it a selectivity for location [13**]. This circuit implements a form of coincidence detection based on excitatory and inhibitory interactions (Figure 1a).

Figure 1



Exploiting first spike latencies in hearing and touch. **(a)** Precise spike timing is used in hearing to localize sound sources. Sound from a source towards the left will excite hair cells in the left ear (L) before hair cells in the right ear (R). Precisely timed excitatory and inhibitory inputs will reach an output cell (O) at different times, determining the strength of the response. **(b)** Potential use of delay lines in touch. Touching an object of a given curvature will excite some tactile afferents earlier than others. Nerve fibers can be exploited as delay lines to detect the specific sequence of afferent firing by neurons in cuneate nucleus.

The sense of touch may deploy an analogous mechanism to rapidly determine the properties of objects upon first contact. Indeed, tactile afferents have been shown to encode information about object curvature [14], the direction at which forces are applied to the skin [15], and the torque applied to the skin [16] (among other features), in the relative latency of their initial responses. Thus, changes in object properties lead to robust and repeatable patterns of relative latencies across afferents with spatially displaced receptive fields [6••]. As with azimuthal location in hearing, then, the information is carried in the *relative* timing of responses across spatially displaced receptors. Thus, to the extent that these highly informative latency patterns are exploited to extract feature information, it is likely that a mechanism akin to interaural time difference detection is involved. A population of coincidence detectors in the cuneate nucleus, the first synapse for touch signals, could in principle extract feature information from patterns of first spike latencies. In fact, a simpler mechanism than that for mammalian auditory localization might be at play in touch. Because the conduction velocities of individual tactile nerve fibers vary over a range [17,18], they naturally act as delay lines; tactile features could therefore be extracted even without the need for precisely timed inhibition, a computation similar to that underlying auditory localization in birds [19,20] (Figure 1b).

Temporal spiking patterns and frequency coding

Acoustic stimuli and skin vibrations

A primary function of the peripheral hearing organ (the cochlea) is to extract information from time varying pressure oscillations, transmitted from the ear drum, through the ossicles, and ultimately transduced in the inner ear.

In touch, the transduction and processing of skin vibrations is, at least at first glance, analogous in that these too carry behaviorally relevant information in their time-varying waveforms [21]. First, just as we can discriminate the pitch of a pure or complex tone, we can distinguish the frequency of a sinusoidal skin vibration, though at a much lower resolution — with Weber fractions of 0.2–0.3 versus 0.003 — and over a much narrower range — up to 1000 Hz versus 20 000 Hz. Second, in both hearing and touch, sinusoidal stimuli can be detected without evoking a pitch percept at low amplitudes, over a range known as the atonal interval [22,23]. The atonal interval coincides with the range of amplitudes over which phase locking of afferents in the nerve is either weak or absent [8]. Third, in both hearing and touch, low frequency stimuli (<50 Hz) elicit a sensation of flutter that is devoid of pitch and in which individual stimulus cycles are discriminable [24,25], while high-frequency stimuli evoke percepts in which individual pulses are fused into a singular percept, to which a pitch can be ascribed [26].

A spatial code for frequency?

A remarkable aspect of hearing is the frequency decomposition engendered by the mechanics of the cochlea: Because the resonance frequency of the basilar membrane progresses systematically along its length, the surface wave produced by a pure tone peaks in amplitude in a different region of the membrane depending on its frequency, with low frequency tones peaking near the apex and high frequency tones peaking near the base. Hair cells in the resonating region respond more than others elsewhere, so different frequencies of stimulation maximally excite different populations of hair cells. Stimulus frequency is thus encoded spatially at the very first stage of auditory processing.

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