Sensing temperature without ion channels

A remarkable gel under the shark's skin enables it to locate prey-rich thermal fronts.

Mammals use cold-sensitive ion channels to translate information about the temperature of their surroundings into electrical signals that are taken up by thermoreceptor nerve cells^{1,2}. Here I investigate the thermoelectric properties of an extracellular gel removed from the electro-sensors of sharks, and show that it develops significant voltages in response to tiny temperature gradients. This bulk property of the gel indicates that temperature can be translated into electrical information without the need for ion channels, a sensitivity that may help sharks to locate thermal fronts as feeding areas.

The ampullae of Lorenzini serve as acute electro-sensors for sharks³ and their relatives, as well as for a few other aquatic predators⁴, but they are also extremely sensitive to abrupt changes in temperature^{5,6}. Gel-filled canals connect each innervated ampulla to pores in the shark's skin. The clear, glycoprotein-based gel has electrical characteristics that are roughly similar to those of a semiconductor⁷, making it a likely medium for strong thermoelectric effects⁸.

Thermopower denotes the strength of the electric-field gradient that is generated by an applied temperature gradient across

a material. I measured the thermopower (also called the Seebeck coefficient, S) for gel samples (2 ml in a quartz container; Fig. 1a) collected from a black-tip reef shark (*Carcharinus melanopterus*) and a white shark (*Carcharodon carcharias*). A temperature gradient was induced by briefly heating one end of the sample holder, and was measured by using platinum thermometers; the resulting change in voltage was monitored by braided silver electrodes (Fig. 1a).

The system then returned slowly to thermal equilibrium (Fig. 1b). The constant voltage offset (usually between -8 mV and $+8$ mV) was presumably due to the resistive gel-electrode interface. Thermopower values were derived from the slope of data collected during heating by standard procedures⁹. Averaging over ten data sets from two samples for each species, thermopower values at room temperature were 370 ± 60 μ V per $^{\circ}$ C for the black-tip reef-shark gel and 240 ± 50 μ V per $^{\circ}$ C for the white-shark gel.

These values indicate that the gel is translating an abrupt thermal stimulus into an electric stimulus in the ampullae. The temperature sensitivity of ampullae (Fig. 1c) excised from dogfish (*Scyliorhinus canicula*) is of the correct order of magnitude⁶ (Fig. 1d)

for it to be explained by a thermoelectric mechanism. Assuming a gradient of 0.1 $^{\circ}$ C across the canal, the S values measured here would give rise to a voltage of roughly 30 μ V within the gel (a drop of 15 μ V in the warmer ampulla, and a rise of 15 μ V rise near the cooler pore). Extrapolating from measurements on the ampullae in the thornback ray (*Platyrrhinoidis triseriata*), a drop of 15 μ V leads to a roughly 300% increase in the firing rate in the associated primary afferent¹⁰, which is consistent with the observed jump for dogfish ampullae.

In a thermopower mechanism, the transient nature of the dynamic temperature response arises from the natural progression to thermal equilibrium. Coupling the thermopower averages (about 300 μ V per $^{\circ}$ C) with the electro-sensory threshold established in behavioural experiments (about 0.05 μ V; ref. 11), the ampullae may even respond to changes of less than 0.001 $^{\circ}$ C. It is not known whether sharks rely on acute temperature sensitivity, but both white and basking sharks (*Cetorhinus maximus*) are able to track marine temperature gradients with precision^{12,13}.

Compared with mammalian cold receptors, the ampullae of Lorenzini are much more sensitive to abrupt cooling, which may reflect different mechanisms of temperature transduction. Some cold receptors in mice rely on a collaboration of multiple temperature-sensitive ion channels². Although this mechanism may operate in neurons associated with the ampullae, it would not account for the sharks' acute temperature sensitivity. As the gel's ion content is not unique⁷, extracellular thermopower may also be important in other biological systems.

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Figure 1 Thermopower and thermal sensitivity of gel samples from shark electro-sensors. **a**, Apparatus used for measuring the gel's thermopower. **b**, The change in voltage with temperature measured in gel extracted from the ampullae of Lorenzini of a black-tip reef shark (samples were collected as described⁷); different curves are obtained for fast heating and subsequent slow cooling (arrows). **c**, Organization of a gel-filled ampulla and canal in the dogfish. **d**, Temperature stimulus and nerve-firing response in dogfish ampulla are shown in the top and bottom curves, respectively (reprinted with permission)⁶; middle curve shows the approximate voltage in the ampulla, calculated from the thermopower data, assuming an exponential decay of the temperature gradient.

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