Report

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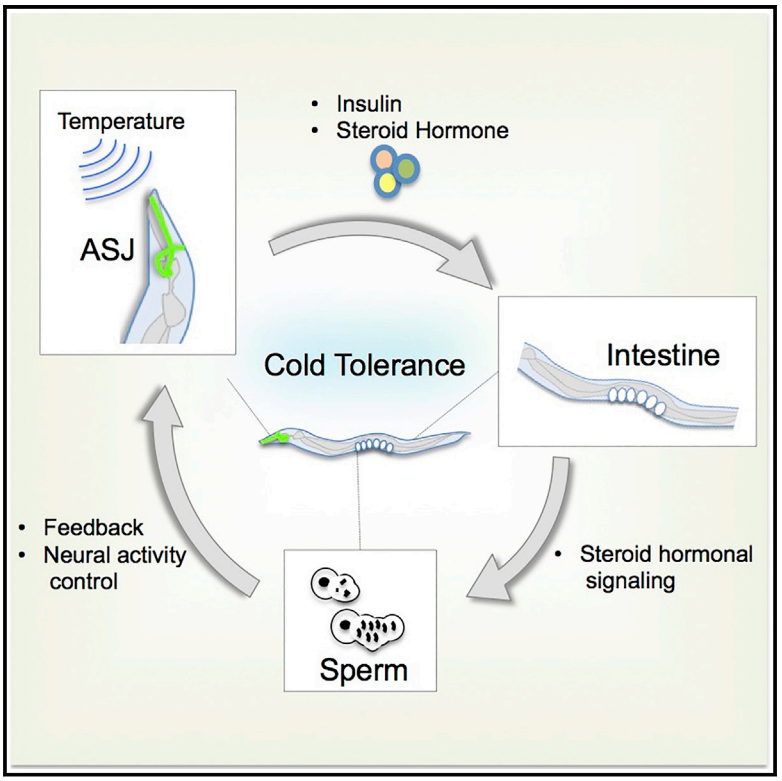
Sperm Affects Head Sensory Neuron in Temperature Tolerance of *Caenorhabditis elegans*

Graphical Abstract



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In Brief

Sonoda et al. find a feedback network between sperm and neurons in cold tolerance of *Caenorhabditis elegans*. ASJ temperature-sensing neurons regulate the intestine through insulin and steroid hormone, which then affects sperm, which, in turn, controls ASJ neuronal activity.

Highlights

- PP1 in sperm is required for cold tolerance
- Sperm is downstream of intestinal insulin signaling in cold tolerance
- Sperm affects the activity of ASJ temperature-sensing neurons
- Steroid-hormone receptors are required for tissue network of cold tolerance

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Sperm Affects Head Sensory Neuron in Temperature Tolerance of *Caenorhabditis elegans*

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SUMMARY

Tolerance to environmental temperature change is essential for the survival and proliferation of animals. The process is controlled by various body tissues, but the orchestration of activity within the tissue network has not been elucidated in detail. Here, we show that sperm affects the activity of temperature-sensing neurons (ASJ) that control cold tolerance in *Caenorhabditis elegans*. Genetic impairment of sperm caused abnormal cold tolerance, which was unexpectedly restored by impairment of temperature signaling in ASJ neurons. Calcium imaging revealed that ASJ neuronal activity in response to temperature was decreased in sperm mutant *gsp-4* with impaired protein phosphatase 1 and rescued by expressing *gsp-4* in sperm. Genetic analysis revealed a feedback network in which ASJ neuronal activity regulates the intestine through insulin and a steroid hormone, which then affects sperm and, in turn, controls ASJ neuronal activity. Thus, we propose that feedback between sperm and a sensory neuron mediating temperature tolerance.

INTRODUCTION

Temperature is an important factor in the survival and proliferation of animals. Growth rates and reproductive efficiencies of invertebrates and many other animals are affected by environmental temperature change. Thus, animals tend to tolerate temperature change using behavioral mechanisms, or they may acclimate by endogenous homeostatic mechanisms, e.g., by changing the fatty acid composition of total lipids and by changing phospholipid saturation (Murray et al., 2007).

Caenorhabditis elegans is a useful model for studying the mechanism of temperature tolerance because of its well-established molecular genetics (Barr, 2003; Brenner, 1974). *C. elegans* is able to change its morphology and behavior in response to environmental temperature change. It is able to alter its temperature-seeking behavior (thermotaxis), depending on cultivation temperature and feeding state (Aoki and Mori, 2015; Ohta and Kuhara, 2013). High temperature induces formation of the dauer larva, which trades arrested development for high-temperature tolerance (Hu, 2007). In contrast to dauer larva formation, *C. elegans* acquires cold tolerance without observable morphological change. A previous report described a pair of temperature-sensing neurons (ASJ) in the head. These neurons are also known to be light- and pheromone-sensing neurons and have been shown to release insulin. Insulin targets the intestine and other neurons. Furthermore, it has been shown that insulin-signaling regulates cold acclimation (Cornils et al., 2011; Liu et al., 2010; Ohta et al., 2014) (Figure 2A). The roles of other tissues in the regulation of cold tolerance in *C. elegans*, however, remain unknown.

One of the most important functions of organisms is reproduction; in many animals, the reproductive machinery is controlled by environmental input via the nervous system (McKnight et al., 2014). For instance, sensory input modulates sperm motility critical for fertilization in *C. elegans*. High population density and food reduction increase synthesis of ascaroside pheromone, which is sensed by ASI sensory neurons, leading to decrease transforming growth factor β (TGF-β) endocrine signaling from ASI neurons. TGF-β directly and indirectly affects prostaglandin synthesis in oogonia, and prostaglandin regulates sperm motility, guiding them to the spermatheca (McKnight et al., 2014). In contrast to dauer larva formation, this sperm-targeting mechanism is not sensitive to temperature (McKnight et al., 2014).

Feedback from somatic cells to neural cells is important for a number of phenomena. The neural circuit underlying aerotaxis in *C. elegans* is modulated by signaling from uterine-vulval cells of the somatic gonad (uv1) through hypoxia-induced factor HIF-1 (Chang and Bargmann, 2008). In thermotaxis of *C. elegans*, neuronal activity of temperature-sensing neuron AFD is modulated by steroid-hormone signaling of estrogen from muscle and intestine (Sugi et al., 2011), in which a nuclear hormone receptor (NHR) acts as a putative estrogen receptor in AFD neurons. However, a feedback system from sperm to sensory neurons has not been reported.

Sperm motility and development are regulated by protein phosphatase 1 (PP1) in mammals (Koch et al., 2015). In *C. elegans,* GSP-4 and GSP-3 encode PP1, which is an ortholog of human PP1-gamma. Both GSP-4 and GSP-3 are expressed specifically in sperm and are required for sperm motility and development (Wu et al., 2012). The motility of nematode sperm depends on the pseudopod rather than flagella. The pseudopod contains major sperm proteins (MSPs), which form the central cytoskeletal element required for actin-independent motility