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Pain in fish: Evidence from peripheral nociceptors to pallial processing

Commentary on [Sneddon et al.](#) on *Sentience Denial*

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Abstract: The target article by Sneddon et al. (2018) presents convincing behavioral and pharmacological evidence that ray-finned fish consciously perceive noxious stimuli as painful. One objection to this interpretation of the evidence is that the fish nervous system is not complex enough to support the conscious experience of pain. Data that contradict this objection are presented in this commentary. The neuroanatomy and neurophysiology of the fish nervous system from the peripheral nerves to the pallium is able to support the sentient appreciation of pain.

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In two recent articles (Woodruff 2017, 2018), I presented neuroanatomical and neurophysiological evidence that the brain of ray-finned fishes is sufficiently complex to support sentience. I did not discuss whether this evidence specifically included the conscious experience of pain. This evidence will be briefly summarized in this commentary.

Sneddon et al. (2018) offer a significant quantity of data leading to the conclusion that sentience in fish includes the experience of pain. Others (e.g., Key 2016; Rose 2007) dispute this conclusion. They claim that all behaviors exhibited by fishes in response to noxious stimuli are reflexive.

Sneddon and her colleagues have shown that A-delta ($A\delta$) fibers associated with fast, sharp pain and C-fibers associated with slow, burning pain are present in the trigeminal nerve of trout (Ashley et al. 2007; Sneddon 2003; Sneddon et al. 2003). However, the density of C-fibers is a fraction of that found in mammals. Rose uses this observation to claim that fish do not consciously suffer from pain, supporting his argument by noting that sea urchin and sea catfish spines are found in the mouths and throats of predatory marine fishes.

However, the combination of the presence of spines in the mouth of fishes and the comparative reduction in C-fibers does not necessarily imply that fish lack the capability to experience pain. Another plausible interpretation is that evolutionary pressure on predatory fishes maximized their ability to select prey by reducing the number of nociceptors in the mouth and throat, areas supplied by the sensory branches of the trigeminal nerve. That this is a reasonable explanation is suggested by the observation that a mutation in the nociceptors of

grasshopper mice renders them impervious to the noxious qualities of the toxin of bark scorpions, one of their preferred foods, while they retain pain-guarding responses to injections of formalin (Rowe et al. 2013).

Electrophysiological studies indicate that fish have functional peripheral nociceptors serving the body and tail. These studies also show that nociceptive input reaches the telencephalon, including the pallium. Dunlop and Laming (2005) recorded neuronal responses to pin-prick to the body of goldfish and trout. Analysis of spike conduction velocities indicated responses to both A δ - and C-fiber activation in the cerebellum, tectum and telencephalon in trout, and in the cerebellum and tectum in goldfish. Interestingly, only longer latency responses attributable to C-fiber activation occurred in the goldfish telencephalon. These data indicate that there is central processing of nociceptive input and suggest a species difference in pain processing in the telencephalon.

Unfortunately, Dunlop and Laming did not specify the location of the telencephalic recording sites. Nordgreen et al. (2007), however, inserted electrodes specifically into the dorsal telencephalon of the Atlantic salmon and recorded sensory evoked potentials (SEPs) to noxious electrical shocks to the tail base. Analysis of the SEPs indicated pallial processing of input originating from A δ - and C-fibers.

Ludvigsen et al. (2014) extended these findings. They recorded tail-shock-induced SEPs from the surface of the skull of Atlantic cod. The amplitudes and latencies of the SEPs indicated pallial responses attributable to peripheral A δ - and C-fiber activation. Ludvigsen et al. also found stimulus-related changes in electrical activity that continued for as long as 240 msec. SEP activity of this duration suggests substantial associative neuronal processing related to elaboration of the nociceptive properties of the stimulus (Zaslansky et al. 1996).

In sum, then, the complexity of neurophysiological activity from peripheral nerves to the pallium supports the argument by Sneddon et al. (2018) that fishes consciously experience pain.

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The Other Minds Problem: Animal Sentience and Cognition

Overview. Since Descartes, philosophers know there is no way to know for sure what — or whether — others feel (not even if they tell you). Science, however, is not about certainty but about probability and evidence. The 7.5 billion individual members of the human species can tell us what they are feeling. But there are 9 million other species on the planet (20 quintillion individuals), from elephants to jellyfish, with which humans share biological and cognitive ancestry, but not one other species can speak: Which of them can feel — and *what* do they feel? Their human spokespersons — the comparative psychologists, ethologists, evolutionists, and cognitive neurobiologists who are the world's leading experts in "mind-reading" other species -- will provide a sweeping panorama of what it feels like to be an elephant, ape, whale, cow, pig, dog, bat, chicken, fish, lizard, lobster, snail: This growing body of facts about nonhuman sentience has profound implications not only for our understanding of human cognition, but for our treatment of other sentient species.

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