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Leaving the door open for fish pain: Evolutionary convergence and the utility of ‘just-so stories’

Commentary on [Key](#) on Fish Pain

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Abstract: Key argues that fish do not experience pain because they lack the necessary (but not necessarily sufficient) brain structures and associated functional circuitry to engender such conscious percepts. I propose that fish pain may be dependent on neuroanatomical regions and pathways that are structurally and/or functionally analogous — but not strictly homologous — to well-characterized mammalian substrates of pain. An example is the convergent appearance of the complex, single-compartment eye across invertebrate and vertebrate phylogeny. Structural-functional convergence is ubiquitous in evolution. Comparative inferences and correlative lines of evidence play an important role in building evolutionary arguments. The dismissal of the perception of pain in fish may be premature at best.

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In the target article, Key (2016a) posits that fish do not experience pain — or any other form of conscious feeling — on the grounds that they do not possess the necessary neuroanatomical structures or functional circuitry to support conscious percepts. This argument has already been made on similar grounds elsewhere (Key, 2015,a,b; Rose et al., 2012). Starting with the human case as a reference standard, Key systematically marshals data from both human and rodent studies to support the claim that a fairly well-defined, evolutionarily conserved constellation of interconnected neural substrates and associated physiological properties in the mammalian brain is the basis for the generation of pain.¹ In making his case, Key points to specific neuroanatomical features in humans and other mammals that make possible the amplification and integration of incoming signals that are thought to be fundamental to conscious processing. These features, he suggests, are absent in fish. He emphasizes the density of feedforward/feedback circuitry in the mammalian cortex, in contrast to the apparent sparseness

¹In his first response to the commentaries, Key (2016b) notes that birds may possess similar neural substrates and might hence be capable of experiencing pain.

of such circuitry in the fish pallium, and notes the role of cortical architecture — specifically, laminar and columnar organization — in differentiating inputs, preserving spatiotemporal relations, and filtering via inhibitory interneuron circuits. The cortex is central to the experience of pain in mammals and its absence, Key claims, indicates the absence of pain and other conscious percepts in fish

Key's main argument is based not just on the lack of cortex in fish, but also on the absence of key functional circuitry associated with the cortex in humans and other mammals, and needed for the perception of pain. This boils down to Key's assessment that there is not enough evidence of structural or functional homology — or, presumably, analogy — to conclude that fish have the requisite circuitry for feeling pain. Key would probably dismiss many appeals to analogy as 'just-so stories.' This is problematic for at least two reasons. First, it discounts the ubiquitous occurrence of structural and functional analogy over the course of evolution. Complex structures with similar properties and functions have often evolved, via different developmental trajectories, from different embryonic tissues, in very different organisms (Conway Morris, 2005; Land and Nilsson, 2012). Analogous structures with similar functions have emerged in different phyla in response to similar ecological challenges. For example, structural and functional similarities to the vertebrate hippocampus have been noted in the neural circuitry subserving memory in certain insects (e.g., honeybees) and cephalopods (e.g., octopus) (Haehnel and Menzel, 2012; Hochner et al., 2006; Menzel and Manz, 2008; Shomrat et al., 2008).

The evolutionary recurrence of the single-compartment, focusing eye is an example of ecologically driven evolutionary convergence not based on homology (except perhaps at the scale of certain conserved photopigment molecules; Fernald, 2006; Land and Nilsson, 2012), but on analogy. This type of eye probably appeared independently in disparate invertebrate and vertebrate species (e.g., coleoid cephalopods, some arthropods, and the vertebrates) more than a half-dozen times over the course of evolution (Land and Nilsson, 2012; Treisman, 2004). The octopus eye is the best example. It closely resembles the vertebrate eye and is similarly capable of resolving both nearby and distant objects (Harland and Jackson, p. 234), making the octopus a superb marine predator. Just as a complex focusing eye evolved independently across different phyla, central processing capable of generating the experience of pain could have evolved independently — through structurally and functionally analogous means — more than once over the course of evolution.

A second reason to resist the temptation to dismiss the possibility of structural-functional analogies is that much of evolutionary biology is predicated on such 'just-so stories.' For a variety of reasons — lacunae in fossil records or technical limits on what is observable — comparative inferences and correlative lines of evidence (i.e., from anatomy, physiology, and behavior) are used to 'bridge the gaps' and supplement the available evidence in evolutionary arguments which often rely on multiple correlative lines of evidence, comparative data, and, to some extent, the very 'just-so stories' Key disparages.

As Key (2016b) observes in his first response to the earlier commentary, the utility of structural-functional analogies such as wings and flight in bats, birds, and insects as justification for the possibility of complex neural faculties (i.e., conscious perception in general and pain in particular) has its limitations. Clearly, bats, birds, and insects all fly — but their means are profoundly different. It could also be argued that the biomechanics of flight is relatively simple in comparison to higher brain function. But the single-compartment, focusing eye is a complex structure that is remarkably similar across vertebrates and certain invertebrates (i.e., coleoid cephalopods; Land and Nilsson, 2012), and necessarily linked to complex visual processing (e.g., decomposition of modal visual properties, integration and binding), regardless of phylogeny. This type of eye provides comparable capabilities (e.g., acuity, spatial resolution, and possibly even stereopsis) in widely different phyla (Harland and Jackson, 2000).

The presence of similar structures in closely related taxa implies phylogenetic conservation of function. In discussing the distinction between parallel and convergent evolution (Arendt and Reznick, 2008; Pearce, 2011) in the elaboration of complex brains, Farris (2015) writes:

“Convergence refers to the independent evolution of similar structures from different ancestral structures and genetic mechanisms, while parallelism occurs when similar structures evolve independently from shared ancestral and genetic mechanisms. Convergence and parallelism can be difficult to differentiate, especially when the phylogeny of the species being compared is incomplete or unavailable.” (Farris, 2015, pp. 1-2)

This difference may be useful in assessing the prospects of investigating the neural substrates for pain in fish. The bony fish (*Osteichthyes*) and mammals (*Mammalia*) can be considered two distinct grades within the clade vertebrata. As vertebrates, members of the two grades share certain neural structures based on their descent from a common ancestor; homologs of mammalian amygdala, hippocampus, thalamus and, of course, brain stem structures have certainly been identified in bony fish. Components of the fish’s pallium seem to be homologous to certain mammalian cortical areas (Segner, 2012). Pain perception in bony fish might have been initiated via circuitry distinct from the mammalian pathways that would emerge much later. The fact that we have not yet identified its neural substrate is insufficient grounds for concluding that fish do not feel pain.

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