

# ANIMAL SENTIENCE

AN INTERDISCIPLINARY JOURNAL ON ANIMAL FEELING

Striedter, Georg (2016) [Lack of neocortex does not imply fish cannot feel pain.](#)  
*Animal Sentience* 3(15)

DOI: 10.51291/2377-7478.1037



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## Lack of neocortex does not imply fish cannot feel pain

Commentary on [Key](#) on Fish Pain

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**Abstract:** Some contemporary scientists are using comparative neurobiological data to argue that non-mammalian vertebrates have feelings, most notably of pain (e.g., Braithwaite, 2010; Mashour and Alkire, 2012), while Key (2016) uses the same general data to reach the opposite conclusion. In a nutshell, he argues that fish cannot feel pain because fish don't have a neocortex, which humans need to consciously experience pain. I don't know how these scientists can look at essentially the same data and reach such disparate conclusions, but I suspect that some of them have strong a priori beliefs and, therefore, view the data through differently tinted spectacles. In any case, I think that both sides have overplayed their hands; the debate cannot be settled yet.

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As Key (2016) notes in his review, teleost fish have brains that differ radically from those of mammals, especially in the forebrain. Teleost fish do have homologs of the main telencephalic divisions that all vertebrates share, but teleosts and other non-mammalian vertebrates don't have the kind of laminated neocortex that mammals possess. Key also claims that humans with extensive damage to the neocortex lack consciousness, including feelings of pain. I am less certain of this claim, in part because the neocortex is such a prominent component of human brains that its destruction is likely to throw most of the remaining central nervous system into paralytic disarray (see Merker, 2007, for additional criticisms of the "consciousness is in the neocortex" argument and Långsjö et al., 2012, for some relevant data). However, for the purposes of argument, I am willing to grant that humans with total neocortical lesions tend not to feel pain. But do these stipulated facts allow us to conclude that fish cannot be conscious or feel pain? I do not think so, because fish might have evolved an altogether different set of neural circuits that is just as capable as the mammalian neocortex of generating consciousness.

After all, the independent evolution of similar neural features and behavioral capacities is a well-known aspect of evolution. It is pretty clear, for example, that the capacity for complex cognition (e.g., tool manufacture and use) evolved independently in birds and mammals (see Striedter, 2013), even though the avian telencephalon is very different from its mammalian counterpart. (Birds do have a neocortex homolog, but most of it differs in numerous respects

from the mammalian neocortex.) Hence we cannot conclude that birds are incapable of complex cognition just because they lack a typical mammalian neocortex. Similarly, we cannot conclude that fish are red-green color blind just because they lack one of the photosensitive pigments that primates need to make this discrimination; fish simply accomplish this task using a different set of molecules (e.g., Bowmaker, 1998). In short, the fact that different species can (and did) evolve different neural mechanisms to achieve similar behaviors makes me wary of concluding that fish cannot feel pain simply because they lack mammalian neocortex.

Key goes on to make a more specific and interesting argument: He claims that having a neocortex is the only way to achieve consciousness, because only a neocortex can provide the kind of “signal amplification” and “global integration” that is needed for consciousness. This is a laudable attempt to specify the kinds of “computations” that might be capable of generating consciousness. However, the criteria he lists seem vague to me and heavily dependent on the assumption that only a mammalian neocortex can generate consciousness, which would make the argument circular. Moreover, it is far from clear that fish brains cannot meet Key’s criteria, because some teleosts have a very well developed telencephalon (Nieuwenhuys, 2009), including lamination in some areas, and all teleosts have a large and highly laminated midbrain tectum, which is generally acknowledged to mediate multisensory and sensorimotor integration (Northmore, 2011), as well as attention (at least in mammals). So, who is to say that a fish brain cannot achieve the kind of signal amplification and global integration that is supposedly sufficient for generating conscious experiences?

Key might counter that possession of a large midbrain is not relevant to the debate, because we already know (or have at least stipulated) that when the neocortex is lesioned in humans the remaining subcortical regions cannot support consciousness. However, ever since Richard Owen introduced the concept of homology into biology, it has been clear that homologous structures may change their functions during the course of evolution (e.g., Striedter and Northcutt, 1991). It is particularly relevant that non-mammals with lesions of the “cerebral hemispheres” have long been known to be capable of broadly conserved behaviors that primates with equivalent lesions cannot perform. For example, fish and frogs are capable of locomotion even after their telencephalon is ablated, whereas primates with lesions of the motor cortex are generally paralyzed (Ch. 2 of James, 1890). Given such species differences in lesion effects, I ask: if fish with without cerebral hemispheres can swim, why shouldn’t they be able to feel pain? It is at least a possibility.

I am also concerned with Key’s claim that non-mammalian vertebrates “do not perform behaviours to be rewarded with pleasurable feelings or alternatively to escape painful feelings.” This claim seems to imply that non-mammals can only generate hard-wired defensive responses to noxious stimuli (nocifensive behaviors), and that they are incapable of behavior that is driven by expected rewards or punishments. Yet it is abundantly clear that both classical and instrumental conditioning are broadly conserved among the vertebrates (MacPhail, 1982). It is interesting to note, for example, that goldfish learn to avoid food that made them nauseous and that this conditioned taste aversion is impaired after telencephalic lesions, just as it is in mammals and birds. Based on his target article, I suspect that Key might respond by saying that

such forms of learning have “survival value” and are, therefore, distinct from conscious feelings. However, I am not convinced that conscious feelings must lack survival value to be considered genuine. Indeed, I would argue that a generalized “feeling of pain” might be just as useful to animals as a highly localized sensation of pain; the latter helps the animal deal with present pain, the former helps it learn how to avoid future pain.

For me, there are two key unanswered questions: First, how does neural circuitry generate consciousness? If we could answer this question, then we could perhaps determine which species have the requisite mechanisms, be they in the neocortex or elsewhere. Alas, I remain unconvinced of any answers that have thus far been proposed. Second, I would like to know what “selective pressures” might give rise to feelings and consciousness, and whether those pressures might differ across species? Again, I do not have a clear answer, but it seems clear to me that pain may have a variety of functions in addition to simply triggering an escape from noxious stimuli. Feelings and memories of pain might, for example, prompt an injured animal to rest and heal, long after the noxious stimulus has passed. Importantly, I’m happy to concede that these functions may vary across species. I am intrigued, for example, by the recent suggestion that humans might feel and express pain differently from other animals, because humans stand to benefit (much more than other animals) when their conspecifics help them recuperate (Finlay and Syal, 2014). However, allowing for this species difference need not imply that non-humans do not feel pain; it simply means that they might feel it differently and, just as importantly, express those feelings differently.

In short, I think that it is possible to analyze feelings of pain (perhaps even consciousness in general) from a comparative perspective, but drawing firm conclusions now seems premature. Hopefully some data from comparative neurobiology can help inform this quest, but I am not yet sure how this might best be done. For now, I remain an optimistic agnostic.

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