

Going beyond just-so stories

Response to Commentary on [Key](#) on *Fish Pain*

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Abstract: Colloquial arguments for fish feeling pain are deeply rooted in anthropometric tendencies that confuse escape responses to noxious stimuli with evidence for consciousness. More developed arguments often rely on just-so stories of fish displaying complex behaviours as proof of consciousness. In response to commentaries on the idea that fish do not feel pain, I raise the need to go beyond just-so stories and to rigorously analyse the neural circuitry responsible for specific behaviours using new and emerging technologies in neuroscience. By deciphering the causal relationship between neural information processing and conscious behaviour, it should be possible to assess cogently the likelihood of whether a vertebrate species has the neural hardware necessary to — at least — support the feeling of pain.

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Just-so stories

In this response to commentaries on the target article “Fish do not feel pain” ([Key](#)), I do not plan to interrogate either the putative behavioural evidence or the just-so stories previously proposed as supportive of fish feeling pain ([Balcombe](#); [Braithwaite & Droege](#); [Broom](#); [Brown](#); [Dinets](#); [Ng](#)). These claims have been adequately addressed and refuted in recent literature (Key, 2015a and 2015b; Rose et al., 2014). It is timely to be reminded of how just-so stories — like those suggesting that it is “obvious” that pain is evolutionary important for all vertebrates ([Brown](#)) or shared by many animals ([Mather](#)), and that active animals need a “certain level of pain” to survive ([Broom](#)) — can easily bias hypotheses and lead to scientists “fooling themselves” (Nuzzo, 2015). [Balcombe](#)’s just-so story about how he can easily “imagine a Tigerfish thinking of swallows as they prepare their next hunting foray” is not helpful to the debate. I intend to move forward and concentrate on the central issue proposed in my paper: that the structure of neural circuits determines the types of computations executed by these circuits and hence the behavioural outcomes. In doing so, I hope to provide a framework for the design of new experiments that more rigorously test hypotheses regarding fish and pain.

What my argument was not

Some commentators incorrectly rearticulated my argument to suggest that any animal without a human cortex can neither exhibit complex behaviour nor feel pain ([Balcombe](#); [Braithwaite & Droege](#); [Brown](#); [Dinets](#); [Haikonen](#); [Jones](#); [Manzotti](#); [Mather](#); [Ng](#); [Striedter](#)). This new and simplified version of my thesis was then subjected to interrogation by the laws of logic ([Jones](#)) as well as by “common sense” ([Balcombe](#)). It was supposedly debunked by analogies, such as jet aeroplanes can fly without propellers ([Ng](#)); and crickets must be deaf because they don’t have human ears ([Dinets](#)). It was supposedly also invalidated by decades of behavioural research demonstrating complex behaviours by many animals, including fish and birds, which lack cortices ([Balcombe](#); [Brown](#); [Seth](#)). One commentator proclaimed my approach was a mere fallacy ([Haikonen](#)).

However, my thesis was never this simple. I clearly sought to define the neural substrates (both anatomical and physiological) that are prerequisites for the feeling of pain in humans. At no time did I say that either these structures or physiological processes were sufficient for pain, and present only in humans. It seems that the field was unprepared for the use of humans as a model system to inform on function in other animals. Interestingly, [Mather](#) warned against relying on what humans report when studying humans.

[Seth](#) claimed that my thesis was “easily challenged by a wealth of evidence from non-mammalian species like birds.” This evidence related to the complex behaviour displayed by these animals. While this statement, by itself, is not very compelling, it does relate to points raised by other commentators who suggested that birds may possess cortex-like neural architecture ([Brown](#); [Striedter](#); [Dinets](#)). Even though these commentators didn’t realise it, this is the very point I was arguing for in my paper. I did clearly articulate “only vertebrate nervous systems possessing all of the following neuroanatomical features are capable of feeling pain.” I proposed that within vertebrates, only those animals with such features are capable — at least — of feeling pain (i.e., those features are necessary but not sufficient). I have also raised this point in another recent article (Key, 2015a) and indicated, very succinctly, that birds appear to possess some of these prerequisite neural properties (even though they do not possess a cortex).

Evidence from mammalian and avian brains supports the structure-function principle

Previous evidence has revealed similarities in the laminar organization of the mammalian cortex and the gross organization of nuclei in the avian auditory pallium (Karten, 2013). This anatomical data is now being supplemented by physiological studies that support the basic premise of my structure-function argument as described in the target article.

During primate and mouse vocalisations, there is motor cortex feedforward input (called corollary discharge) that suppresses the auditory cortex (Eliades and Wang, 2008; Nelson et al., 2013; Schneider et al., 2014). This motor-elicited suppression involves a circuit consisting of excitatory motor cortical projection neurons terminating on

inhibitory interneurons in the auditory cortex. This neural mechanism seems to be very important in self-monitoring, vocal learning and distinguishing self from externally produced auditory inputs (Schneider and Mooney, 2015). Interestingly, songbirds have motor pallial projection neurons that also carry corollary discharge to the auditory pallium and this activity is involved in vocal learning. Thus, primates, mice and songbirds possess similar basic local and long-range circuitry in the auditory cortex and auditory pallium, and they share similar functional properties involved in specific hearing behaviours.

Recently, the basic premise of the structure-function relationship was examined at the level of canonical microcircuits in the avian auditory pallium (Calabrese and Woolley, 2015). Birds demonstrated hierarchical information processing, response features and population coding in the auditory pallium similar to that previously described in mammalian auditory cortex in response to auditory stimuli. These results support the idea that structurally analogous microcircuits perform similar high-level functions across these vertebrate species. Of course these structure-function relationships do not address whether the songbirds are consciously aware of their vocalisations. More detailed analyses obviously need to be completed in order to begin to understand whether such brain regions also support global integration and signal amplification underlying phenomenal consciousness. Nonetheless, these studies are providing positive signs that similar neural architectures can be used to predict analogous physiological functions and most likely high-level brain behaviours within the vertebrate lineage.

Other-brain-regions argument

A common dismissive approach to my argument was to claim that “other brain regions” are clearly able to produce the sensation of pain in fish. This proposition arises from the idea that throughout the animal kingdom many different anatomical structures seem to perform similar physiological functions. However, the anecdotes presented were typically simple and lacked critical insight. For instance, [Manzotti](#) noted that bats can fly without feathers. My response to such an analogy is that one needs to understand how feathers enable flight (e.g., what are their aerodynamical properties and how are they structurally arranged to produce flight). In this case, it is important to note that different feather structures as well as their particular arrangement can produce different flight behaviours in birds (Beaufrère, 2009; Xu et al., 2014; Chen et al., 2015). Moreover, birds and bats exhibit very different flying behaviours because of their different anatomies (Hedenström et al., 2007; Hedenström and Johansson, 2015). Once the fundamental aerodynamical principles of feathered flight have been characterised (just as I defined the fundamental neural principles in human pain), then one could search for their structural basis in other species (e.g., bats). That is, do bats have similar anatomical structures that permit feathered flight or do they produce a very different type of flight because of anatomical differences? What proponents of the “other brain regions” argument fail to do is to progress their reasoning to a mechanistic level (both anatomical and physiological). Rather than understand how other brain regions could, or could not, lead to pain, they instead superficially treat these structures as “black boxes.”

[Striedter](#) argues that homologous brain regions can perform different functions in different species. He cites the observation that fish can swim in the absence of the

telencephalon, but primates with motor cortex lesions are paralyzed. By inference, lower brain regions produce locomotion in fish, but not in humans, so perhaps fish can also feel pain within these regions. Once again it is imperative to interrogate the underlying neural architecture and circuitry in order to address this matter. Rhythmical locomotion in vertebrates depends on central pattern generators (Marder and Bucher, 2001; Jung and Dasen, 2015). Some of these generators are present in the brainstem and spinal cord, and their control is regulated to varying extents by higher-level circuitry in different species. The distinct body postures adopted by humans with lesions in different brain regions reveals that hierarchical control mechanisms modulate the spinal cord central pattern generators (Schepelmann, 1979). Nonetheless, the basic structure and function of these central pattern generators remain very similar across vertebrate species. For instance, when either a spinal dog or cat is placed in a harness to support their body weight, these pattern generators can be activated to generate locomotor behaviours. To conclude, as [Striedter](#) does, that fish lower brain regions and spinal cords are doing something remarkably different is merely misunderstanding the underlying anatomy. Once again, critical insight is gained by examining the neural structures in detail (as I argued in the target article). In fact, the cortical control of motor activity raised by [Striedter](#) is more consistent with the argument that the cortex has specialised neural functions.

Rather than discuss the validity of my proposed anatomical and physiological prerequisites for pain, some commentators instead proposed that pain is such an important behaviour that it must be central to both the evolution of all vertebrates ([Brown](#)) and to the “flexible and adaptive behaviour” demonstrated by fish ([Seth](#)). Consequently, these just-so stories can lead to the conclusion that pain must have evolved early in the vertebrate lineage, and must be localised to an anatomical structure present in most, if not all, vertebrates. The phylogenetically old brainstem ([Ng](#)) and/or the midbrain tectum ([Striedter](#)) were presented as possible brain regions. [Seth](#) also suggested that fish pain was occurring in some “phylogenetically ancient brain region” with “alternate neuronal architectures.” It is interesting that none of the commentators actually proposed what those alternate neural circuits could be in these ancient brain regions. One commentator went as far as to suggest that neural processes do not underlie pain ([Manzotti](#)). It needs to be pointed out that [Braithwaite & Droege](#) did acknowledge that both global integration and attentional amplification are “essential elements in consciousness” as I argued. Unfortunately, they then automatically assumed that the fish brain must possess the necessary neural architecture to execute these functions.

Preoccupation with complex behaviours

Some commentators argued that complex behaviours demonstrated by animals is clear evidence, in itself, of animal consciousness and hence their ability to feel pain. Many of these behaviours are presented as just-so stories, for example: the big grouper cleaning stations ([Dinets](#)), fish learning about food sources ([Broom](#)), tool use ([Seth](#)), bird-hunting fish ([Balcombe](#)), nausea-causing taste aversion in goldfish ([Striedter](#)), and zebrafish learning from fear ([Broom](#)). [Braithwaite & Droege](#) have called for more behavioural measures to be used in order to further demonstrate conscious pain in fish. However, they mistakenly claim that I also advocate better tests (such as those involving the loss of normal behaviour) as evidence of pain. Unfortunately, my argument was

misinterpreted. What I actually demonstrated was that if such an approach were adopted (e.g., operations on fish involving craniotomy), it would be found insufficient. I also argued that some seemingly complex behaviours can be executed without the need of pain for motivation. One example I highlighted was the ability of a rodent spinal preparation to control leg position so as to prevent getting an electric shock.

In his commentary, [Hart](#) raised the idea that there is a strong belief by some biologists that complex behaviour automatically implies consciousness. He suggested that this idea emerged from the subjective experience that consciousness seems to be central to human complex behaviours. Typically these complex behaviours are considered to be goal-directed and flexible (i.e., ability to modify behaviour in novel circumstances; Waskom et al., 2014). Since goal-directed behaviour is usually thought to involve the conscious appreciation of the relationship between a stimulus, a response (or action) and an outcome (Wokke et al., 2011; Zwosta et al., 2015), it becomes clear why fish behaviourists emphasise the ability of fish to perform complex behaviours as evidence for fish consciousness. Moreover, in many cases pursuing goals also seems tightly associated with being aware of (i.e., to feel) rewards and/or punishments (Dijksterhuis and Aarts, 2010). Consequently, questioning the idea that fish feel pain seems to be interpreted by some behaviourists as an attack on the ability of fish to perform complex behaviours. Breaking the link between goal pursuit and consciousness (Williams et al., 2009; Wokke et al., 2011; van Gaal et al., 2012; de Pisapia, 2013; Tamir et al., 2013; Huang and Bargh, 2014) may lead to a new way of thinking about fish behaviour. In this respect, I would like to highlight recent research that is probing how some human behaviours, such as the placebo and nocebo effects as well as pain conditioning (which were previously considered to be dependent on conscious will or awareness) can be explained by nonconscious processes. These studies are clearly revealing that the link between the execution of complex behaviour and conscious expectancies or feelings is not necessary to explain outcomes (Jensen et al., 2012, 2015a and 2015b).

[Chella](#) introduces a new line of experimental evidence that questions the need for conscious neural processing in fish behaviour. He discusses how robotic fish can perform complex behaviours based on automatic stimulus-response processing without cognitive architectures. However, he does carefully acknowledge that robotic fish are not real fish and what this research is showing, at least, is that adding the capacity of feeling to robotic fish may not change their behavioural repertoire. Nonetheless, robotics is an exciting area of research and recent advances in the autonomous behaviour of mobile animal-like robots (Bazeille et al., 2014) may in the future provide some novel insights into the types of neural processing required for complex animal behaviours. It is also important to highlight complementary research aimed at generating computational models of the human brain (Eliasmith et al., 2012; Rasmussen and Eliasmith, 2013). Such models are able to perform complex tasks involving memory, visual perception and reasoning and are built on the principles of brain-like neural information processing. If we assume that these stimulations are not conscious, then the mandatory link between awareness and complex behaviour dissolves.

The way forward

In addition to changing the way we think about associating consciousness and complex behaviours, it is imperative that the practice of representing brain regions as mysterious

black boxes is abandoned. I proposed that structure determines function and that this is applicable to the level of neural circuits controlling behaviours. Many commentators proposed (without evidence) that different structures (i.e., brain regions) can perform the same function. That is, the brainstem in fish can do what the cortex does in mammals. The field needs to move forward and go beyond this black-box approach to brain function and, at least, attempt to define the nature of the circuitry within the brainstem that is executing the computations proposed to be responsible for the feeling of pain. It is not enough to merely claim via analogy that “propellers” and “jet engines” do the same thing ([Ng](#)). If we persevere with the same analogy: where is, and what is, the “propeller” in the brainstem and how is it achieving the same function as the “jet engine” in the cortex.

The present and next generation of fish behaviourists must be encouraged to embrace state-of-the-art neural recording and imaging approaches and molecular genetic manipulations that are allowing the dissection of the neural circuits responsible for mammalian behaviours (Choi et al., 2011; Franks et al., 2011; Gaykema et al., 2014; Land et al., 2014; Betley et al., 2015; Graebner et al., 2015; Vardy et al., 2015). It is an opportune time to combine electrophysiological and advanced microscopy techniques with neural circuit manipulation and mapping approaches to establish the causal link between neural activity and specific behaviours. Such strategies should cast light on what neural architectures underlie awareness and could possibly lead to novel ways of directly altering circuit function (Krug et al., 2015; Saunders et al., 2015) so as to modulate pain.

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