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Contemporary topics in fish cognition and behaviour

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The field of fish cognition and behaviour is now well established and recent developments reflect a shift to mechanistic, comparative and theoretical approaches compared to early work. In this review we briefly summarise recent advances in four major areas of research: spatial learning, social cognition, numerical competency and cognition, consciousness and pain. The debate on whether fish are conscious and able to feel pain is particularly topical, and we discuss recent behavioural and adaptive arguments in favour of fish pain. In this review we also propose interesting avenues of research in which fish have been given little attention in comparison with other vertebrate species.

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Introduction

Fish have now become a standard model species in the study of comparative cognition (Figure 1). Comprehensive reviews on fish behaviour and cognition, with detailed methodologies used in this research, are available and we refer readers new to this field to those reviews [1,2••,3••,4]. The objective of this short review is to summarise developments in four major areas of contemporary research in fish cognition, as well as highlight some exciting new directions in less studied topics (Box 1).

Numerical discrimination

Numbers are an essential part of everyday life for most animals. Being able to count or assess quantities can guide decisions such as which group to join, where to forage or whether to fight or flee (see Ref. [5]). This is also true for fish, and indeed they show good numerical skills. The main focus of research in numerical competency in fish has been to distinguish quantity discrimination from numerical abilities (by controlling other cues that covary with numerosity), understand the accuracy and upper limit of their discrimination ability, and assess how fish compare to other vertebrate species (reviewed in Ref. [6]). The general consensus from this work is that fish have good number sense and can be as efficient in establishing quantity as terrestrial vertebrates.

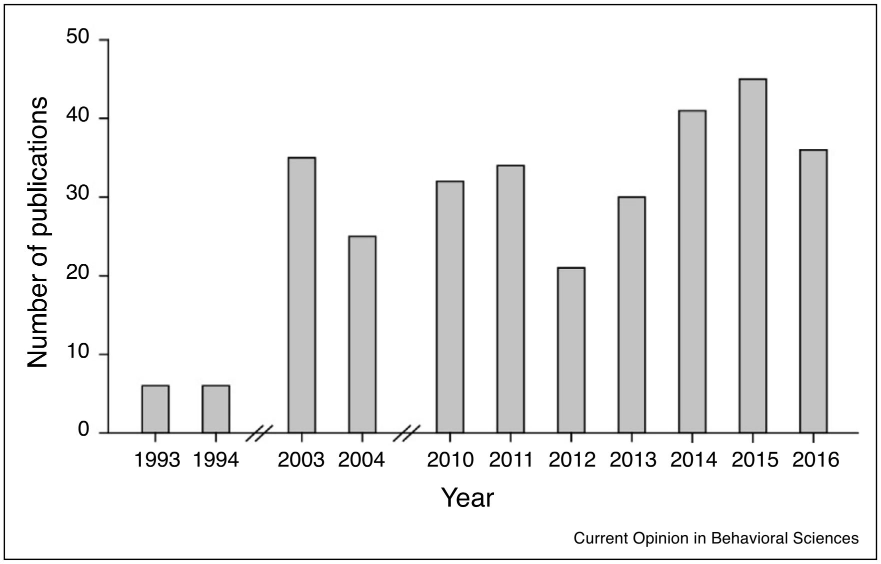
Two numerical information processing systems seem to exist in humans: a generalist 'analogue magnitude system' to estimate large quantities; and an accurate 'object tracking system', to quickly track small quantities individually. Recent studies have sought to understand if these also occur in fish (reviewed in Ref. [6]). In line with other non-human animals, some studies on fish support the dual system hypothesis (*e.g.* [7]), and the unit limit of the 'object tracking system' of fishes seems to be similar to other vertebrates (around four objects, set by short-term memory). Nonetheless, a few studies provide support for an alternative perspective, that a single processing system could operate across all quantities (*e.g.* [8,9]), thus leaving the subject unresolved and open to further study.

Fish are capable of true numerical discrimination like other species, but will spontaneously use continuous quantities if available [10,11]. Their accuracy and upper discrimination limit is comparable to those of mammals and birds, with some species-specific differences [6,12–15]. Three-spined sticklebacks, for example, were successful in a discrimination task where they choose the larger of two social groups with a ratio of 0.86 (*i.e.* there is small relative difference between quantities), similar to bottlenose dolphins [8,16]. It also appears that, when learning to distinguish between quantities, fish spontaneously learn about relative sizes (this is bigger than that) instead of absolute sizes (this has four elements and that has two), even though they are capable of both [17], and can even learn using ordinal numerical information (choose the *n*th element; [18]).

Researchers have also begun investigating proximate mechanisms of numerical discrimination such as the role of individual, sex, cerebral lateralization and context differences [9,13,19,20]. For example, guppies that were strongly lateralized had better numerical skills than non-lateralized fish, both in the context of shoal size choice and training with abstract stimuli [20], and their numerical acuity was enhanced when two guppies were interacting, as a result of meritocratic leadership [21].

Another emerging theme in human and non-human literature is whether numerical discrimination is independent of sensory modalities. Evidence in other species is

Figure 1



The number of publications on fish learning and cognition grew in recent decades and currently seems to be reaching stability. Data based on keyword search (fish, fishes, learn, learning and cognition) in Google Scholar. The 2016?data excludes publications from November and December.

still inconclusive [22], and in fish only one study has addressed this issue. Blind cavefish could distinguish between groups of sticks up to a ratio of 0.50 (two versus six and two versus four sticks), but were unsuccessful when tested with a 0.67 ratio (two versus three sticks), a ratio achieved by other fish species using vision [14]. These results are compatible with the idea of multiple modality-dependent systems for numerical skills in fishes but far more work needs to be done in this area [14]. It is also a possibility that specific selective pressures acted on blind cavefish to decrease metabolic consumption, reducing brain mass or dropping neural circuits related to cognitive tasks not useful in caves, such as shoal size discrimination [14]. One good approach to tackle ultimate and proximate questions for numerical discrimination would be to use species that are active in both good and poor light conditions, such as weakly electric fish, and test them with visual and other sensory cues [14].

Box 1 New lines of research in fish cognition.

Cognitive flexibility is one emergent area of research. While only a few species have been studied, it seems fish are capable of inhibiting previously learned behaviours, of reversal learning (*e.g.* [58]), and display innovative behaviours and problem solving in new situations (*e.g.* [59]). Fish would be a good model species to test evolutionary ecology predictions such as the 'necessity drives innovation' hypothesis, and investigate potential mechanisms underlying behavioural flexibility [60,61].

Another topic largely unexplored is the study of play behaviour in fish. For long deemed restricted to primates, it has become clear other species of mammals and birds also play. Playful behaviour seems to be a developmental precursor to many behavioural and social skills, and might facilitate innovation and creativity [62]. Since the observation of fishes' natural behaviour is rare compared to other vertebrates, and a generic definition of play applicable throughout the animal kingdom has been controversial, early claims of play in fish have largely been dismissed [63]. However, Burghardt and colleagues have recently proposed a 'five criteria' definition of play that can also be applied to fish, amphibians and reptiles [62,63], and have reported a peculiar thermometer-striking behaviour in cichlid fish that fits the play definition [64]. Because of the diversity and sophistication of behaviours and cognitive abilities of fishes, it seems only reasonable to assume play behaviour also occurs in fish and thus should be further investigated.

Social cognition

Complex social intelligence is no longer considered restricted to primates. Complex social behaviours in fish have been widely acknowledged and reviewed and include social learning and traditions, individual recognition, cooperation and shared intentionality, dominance hierarchies, social status and transitive inference, among many others [1,4].

Fish are an ideal group to test ecological and evolutionary links to social cognition. Most species differ in social and/or ecological complexity in the wild, and we can easily manipulate their social experiences or information perception in the laboratory to disentangle some of these interactions (*e.g.* [23,24]). Moreover, we know the biological functions and metabolic needs driving many social behaviours are highly conserved across vertebrates, as are neuromolecular pathways and neural circuits for social decision making [25–27]. Armed with this recent knowledge, now is an exciting time to study fish social cognition using comparative approaches.

Similar to humans and other primates, fishes' social behaviour and decision-making processes are linked to molecular and gene expression changes (*e.g.* [28•,29,30]). For example, the decision to cooperate or cheat and the perception of reward in cleaner wrasses is modulated by cortisol, dopamine and the neuropeptide arginine-vasotocin [31–33], that are also involved in similar behaviours in monkeys [34]. In Tanganyikan male ciclids, gaining or losing dominance is related to an increase or decrease of neuron volume, respectively [28•]. Similar relationships have been found in primates [35,36].

While we have learned a lot by looking at specific species and isolated social behaviours like cooperation and aggression across functional contexts, in the wild many of these behaviours and decision processes overlap. Moving forward we need to combine these social behaviours within theoretical frameworks of optimality and 'evolvability', and integrate the proximate mechanisms underlying behaviour into our current models [37••]. While a challenging task, models and experiments should start to incorporate variation in game structures and pay-off matrices (*e.g.* combining a prisoner's dilemma and a by-product mutualism game), to consider individual behavioural variation due to personality, for example, or that allow pay-off matrices to evolve from positive feedback-loops due to selection for some behaviours (*e.g.* social competence) [37••].

Spatial cognition

Fish have long been used as a model species for understanding the evolution of spatial learning and memory (see Ref. [1]). Of course, many fish operate in three dimensions thus there is good reason to believe that depth, as perceived through baroreceptors, is an important component of the fishes' spatial world. Recent experiments using a rotating t-maze showed that fish are better at extracting the depth component than the horizontal component when they had to recall the position of a reward in three dimensional space [38]. Moreover, they separate the two components and tend to prioritise the vertical component of a spatial task over the horizontal component when both cues are in conflict [39]. Interestingly, the errors made during recall in the vertical and horizontal axes are roughly the same suggesting the fish have a supramodal representation of their world that is similar in both vertical and horizontal planes [40•]. In the context of the neurological mechanisms, one would predict that the place-cell fields in fish would be similar to bats, but this has yet to be determined [40•].

There has been much interest in the environmental correlates of spatial learning and emphasis on the ecological cognition hypothesis [41]. The theory poses that the learning and memory skills of an animal are sharply honed by the selective pressures operating in a species microhabitat. In a series of papers, White and Brown compared the spatial learning ability of intertidal gobies from sandy shores versus rocky reefs ([42–44,45•]; Figure 2). Gobies from stable rocky shores need to have great spatial learning abilities to ensure they return to the home pool at each low tide to avoid being stranded. Gobies from sandy shores, by contrast, need only retreat with the tide. Reef gobies have very high site fidelity to their home pools and rapidly return after displacement [44]. In artificial rock platforms, rocky reef gobies rapidly discovered the location of a deep pool refuge whereas sand dwelling gobies followed the tide out and were repeatedly stranded [42]. Rocky reef gobies found the location of food rewards in a radial maze much faster than sandy shore gobies and tended to use both landmarks and egocentric, turn based cues ([43], Figure 2d,e). Analysis of the gobies' brains showed that the rocky reef gobies had a significantly larger telencephalon, the brain region responsible for spatial learning, than sandy shore fish ([45•], Figure 2a,c). These findings closely mimic those found in caching and non-caching species of birds [46] and mammals [47].

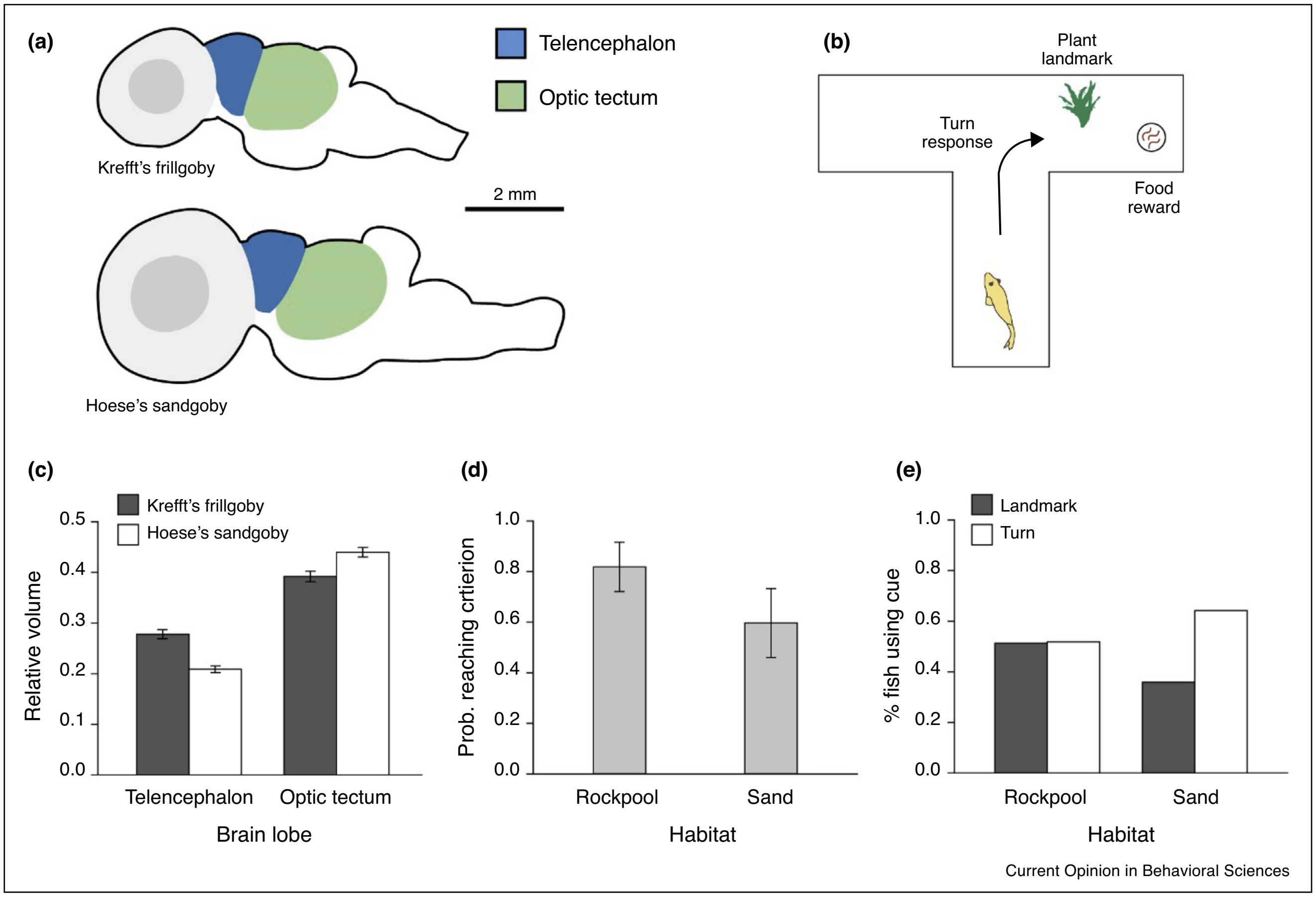
Personality traits also seem to shape spatial learning abilities, along with other cognitive traits, yet exactly how they are linked is still uncertain (Box 2).

Cognition, sentience and pain

Brown [3••] has previously outlined the link between cognition, sentience and ethics and there is growing consensus that fish can respond to pain emotionally in a manner similar to other vertebrates. From an evolutionary perspective, there is little reason to believe that the detection of painful stimuli (nociception) should be separated from the emotional responses to those stimuli [48••,49••]. Clearly the adaptive benefits from a pain perception system is that animals are able to respond immediately (*e.g.* via reflex) to withdraw from painful stimuli and, importantly, remember that situation or context so they may prevent such encounters in future. There is little doubt that the latter requires cognitive engagement and particularly an emotional response to the negative stimuli (*e.g.* fear) as a key driver for memory formation. Learning, memory and the emotional drivers are, therefore, important components of pain and all of them are present in fish.

A minority have challenged the notion that fish feel pain because they are not conscious [50,51]. In the most recent paper, Key [51] concludes that any animal lacking a human-like cortex is incapable of consciousness and thus does not feel pain. Quite clearly an argument along these lines is nonsensical and ignores the fact that fish and other vertebrates use other parts of their brain to analyse pain,

Figure 2



Brain morphology, habitat complexity and spatial learning abilities are related in intertidal gobies [42–44,45•]. **(a)** Schematic representation of the brains of Krefft's frillgoby *Bathygobius krefftii* which dwells in rockpools (top) and Hoese's sandgoby *Istigobius hoese* which lives on sandy intertidal areas (bottom), showing the location of the telencephalon and optic tectum (modified from Ref. [45•]). **(b)** Simplified diagram of the T-maze used in spatial learning tasks. **(c)** Comparison of relative brain lobe volumes (mean ± SE) between two goby species from different habitats. **(d)** Mean (±SE) probability of fish reaching learning criterion in a T-maze task for rock pool and sand-dwelling species. **(e)** Proportion of rock pool and sand-dwelling fish using plant landmarks and turn direction for orientation during probe trials.

and part of this response may have been co-opted by the mammalian cortex over the course of evolution [48••]; see also responses to Key's article in the same issue]. Similarly, vision is processed in the human cortex but in most other vertebrates it occurs in the optic lobes. Does that mean other vertebrates are blind? Moreover, the avian cortex, for example, is widely accepted as the mammalian functional equivalent to the mammalian cortex but has a unique evolutionary origin and organisation.

Sneddon has repeatedly outlined the substantial evidence that fish feel pain in a manner similar to mammals (*e.g.* [49••]). It is clear that the physiology and anatomy is highly conserved across vertebrates, the behavioural response to pain mimics that seen in mammals and symptoms can be alleviated by the application of analgesics. More recently, Rey *et al.* [52] have also found evidence of 'emotional fever' in zebrafish following confinement within a small net (2–4°C above control fish) contrary the original findings of Cabanac and Laberge [53]. During times of emotional stress or anxiety, mammals develop a fever, with a physiological response

Box 2 Cognition as a proximate cause of personality.

Individual differences in behaviour are often considered in behavioural ecology studies. It seems that in fish personality is linked to many aspects from cerebral lateralization to aggression and learning [1]. For example, there is emerging evidence that personality shapes spatial learning in fishes, particularly the trade-off between speed and accuracy. But the nature of this interaction in fishes is currently equivocal. Shy trout had faster learning rates than bold trout in a spatial learning task [65]. In contrast, bold guppies learnt a simple spatial task faster and more accurately than shy guppies [23]. To further muddy the waters, bolder sticklebacks made faster decisions in a t-maze task but were less accurate than shy sticklebacks [66]. Evidently far more research needs to be conducted in this area.

and symptoms equal to those induced by pathogens. Emotional fever has been reported in humans in the lead up to stressful events such as sitting exams [54]. The body temperature of rats [55] and lizards [56], for example, also increases in response to handling. Ectotherms generally show fever by behavioural thermoregulation; choosing to spend more time in warmer microhabitats. While the relationship between emotion and consciousness is still debated, Rey *et al.*'s finding removes an argument often cited for lack of consciousness in fishes.

Interestingly, there was considerable individual variation in how zebrafish responded to the stressor and displayed emotional fever. Recent papers show that personality type can influence thermal preferences in fish [57], thus it seems highly likely that personality may also play a role in shaping emotional fever responses in fish.

Fish are widely used for scientific research, are the most consumed animal in terms of numbers and the most numerous pet. The ethics and welfare implications of such a debate on sentience and pain are therefore great. As Brown [3••] highlights, notwithstanding the complexity of the debate and whether we have definitive answers, current knowledge on their cognitive sophistication and pain perception suggests that the best approach is to give them the same welfare protection as any other vertebrate. Gaining further understanding of the sophisticated cognitive abilities of fish will undoubtedly contribute to this ongoing debate.

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Brown C, Laland K, Krause J (Eds): *Fish Cognition and Behavior*. Blackwell Publishing; 2011.

2. •• Patton BW, Braithwaite VA: **Changing tides: ecological and historical perspectives on fish cognition**. *WIREs Cogn. Sci.* 2015, **6**:159-176.

This paper summarizes some of the history of the field of fish cognition, and in light of its continuing expansion highlights the necessity of cognitive research based on the ecological and evolutionary context of species, to further understand fish cognitive abilities and develop sound predictions and theory in the overall field of cognitive science.

3. •• Brown C: **Fish intelligence, sentience and ethics**. *Anim. Cogn.* 2015, **18**:1-17.

In this review, the current state of knowledge on fish sensory and cognitive abilities and evidence for pain perception are compiled, revealing that fish often match or exceed other vertebrates and building a solid case in favour of fish sentience and consciousness with big welfare implications.

4. Bshary R, Brown C: **Fish cognition**. *Curr. Biol.* 2014, **24**: R947-R950.

5. Shettleworth SJ (Ed): *Cognition, Evolution, and Behavior*. Oxford University Press; 2010.

6. Agrillo C, Petrazzini MEM, Bisazza A: **At the root of math: numerical abilities in fish**. In *Evolutionary Origins and Early Development of Number Processing*, vol. 1. Edited by Geary DC, Berch DB, Koepke KM. Academic Press; 2014:3-34.

7. Agrillo C, Petrazzini MEM, Bisazza A: **Numerical acuity of fish is improved in the presence of moving targets, but only in the subitizing range**. *Anim. Cogn.* 2014, **17**:307-316.

8. Mehlis M, Thünken T, Bakker TC, Frommen JG: **Quantification acuity in spontaneous shoaling decisions of three-spined sticklebacks**. *Anim. Cogn.* 2015, **18**:1125-1131.

9. Petrazzini MEM, Agrillo C: **Turning to the larger shoal: are there individual differences in small-and large-quantity discrimination of guppies?** *Ethol. Ecol. Evol.* 2015, **28**:211-220.

10. Agrillo C, Dadda M, Serena G, Bisazza A: **Use of number by fish**. *PLoS One* 2009, **4**:e4786.

11. Agrillo C, Piffer L, Bisazza A: **Number versus continuous quantity in numerosity judgments by fish**. *Cognition* 2011, **119**:281-287.

12. Potrich D, Sovrano VA, Stancher G, Vallortigara G: **Quantity discrimination by zebrafish (*Danio rerio*)**. *J. Comp. Psychol.* 2015, **129**:388.

13. Lucon-Xiccato T, Dadda M, Bisazza A: **Sex differences in discrimination of shoal size in the guppy (*Poecilia reticulata*)**. *Ethology* 2016, **122**:481-491.

14. Bisazza A, Tagliapietra C, Bertolucci C, Foà A, Agrillo C: **Non-visual numerical discrimination in a blind cavefish (*Phreatichthys andruzzii*)**. *J. Exp. Biol.* 2014, **217**:1902-1909.

15. Gómez-Laplaza LM, Gerlai R: **Discrimination of large quantities: Weber's law and short-term memory in angelfish, *Pterophyllum scalare***. *Anim. Behav.* 2016, **112**:29-37.

16. Jaakkola K, Fellner W, Erb L, Rodriguez M, Guarino E: **Understanding of the concept of numerically less by bottlenose dolphins (*Tursiops truncatus*)**. *J. Comp. Psychol.* 2005, **119**:296.

17. Petrazzini MEM, Agrillo C, Izard V, Bisazza A: **Relative versus absolute numerical representation in fish: can guppies represent "fourness"?** *Anim. Cogn.* 2015, **18**:1007-1017.

18. Petrazzini MEM, Lucon-Xiccato T, Agrillo C, Bisazza A: **Use of ordinal information by fish**. *Sci. Rep.* 2015, **5**:15497.

19. Thünken T, Eigster M, Frommen JG: **Context-dependent group size preferences in large shoals of three-spined sticklebacks**. *Anim. Behav.* 2014, **90**:205-210.

20. Dadda M, Agrillo C, Bisazza A, Brown C: **Laterality enhances numerical skills in the guppy, *Poecilia reticulata***. *Front. Behav. Neurosci.* 2015, **9**.

21. Bisazza A, Butterworth B, Piffer L, Bahrami B, Petrazzini MEM, Agrillo C: **Collective enhancement of numerical acuity by meritocratic leadership in fish**. *Sci. Rep.* 2014, **4**.

22. Tokita M, Ashitani Y, Ishiguchi A: **Is approximate numerical judgment truly modality-independent? Visual, auditory, and cross-modal comparisons**. *Atten. Percept. Psychophys.* 2013, **75**:1852-1861.

23. Trompf L, Brown C: **Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata***. *Anim. Behav.* 2016, **88**:99-106.

24. Hotta T, Takeyama T, Heg D, Awata S, Jordan LA, Kohda M: **The use of multiple sources of social information in contest behavior: testing the social cognitive abilities of a cichlid fish**. *Front. Ecol. Evol.* 2015, **3**.

25. Weitekamp CA, Hofmann HA: **Evolutionary themes in the neurobiology of social cognition**. *Curr. Opin. Neurobiol.* 2014, **28**:22-27.

26. Bshary R, Gingins S, Vail AL: **Social cognition in fishes**. *Trends Cogn. Sci.* 2014, **18**:465-471.

27. O'Connell LA, Hofmann HA: **Evolution of a vertebrate social decision-making network**. *Science* 2012, **336**:1154-1157.

28. Fernald RD: **Social behaviour: can it change the brain?**
• *Anim. Behav.* 2015, **103**:259-265.

This paper reviews and unifies work on a fish model species to investigate how social interactions and dominance hierarchies modulate fish brain structure and gene expression patterns, and in turn alter the behaviour of animals as they interact.

29. Teles MC, Almeida O, Lopes JS, Oliveira RF: **Social interactions elicit rapid shifts in functional connectivity in the social decision-making network of zebrafish**. *Proceedings of the Royal Society B: The Royal Society* 2015.

30. Soares MC, Bshary R, Fusani L, Goymann W, Hau M, Hirschenhauser K, Oliveira RF: **Hormonal mechanisms of cooperative behaviour**. *Philos. Trans. R. Soc. B: Biol. Sci.* 2010, **365**:2737-2750.

31. Soares MC, Cardoso SC, Grutter AS, Oliveira RF, Bshary R: **Cortisol mediates cleaner wrasse switch from cooperation to cheating and tactical deception**. *Horm. Behav.* 2014, **66**: 346-350.

32. Messias JPM, Paula JR, Grutter AS, Bshary R, Soares MC: **Dopamine disruption increases negotiation for cooperative interactions in a fish**. *Sci. Rep.* 2016, **6**:20817.

33. Cardoso SC, Paitio JR, Oliveira RF, Bshary R, Soares MC: **Arginine vasotocin reduces levels of cooperative behaviour in a cleaner fish**. *Physiol. Behav.* 2015, **139**:314-320.

34. Schultz W: **Dopamine signals for reward value and risk: basic and recent data**. *Behav. Brain Funct.* 2010, **6**:1-9.

35. Kanai R, Bahrami B, Roylance R, Rees G: **Online social network size is reflected in human brain structure**. *Proceedings of the Royal Society B: The Royal Society* 2011. rspb20111959.

36. Sallet J, Mars R, Noonan M, Andersson J, O'reilly J, Jbabdi S, Croxson P, Jenkinson M, Miller K, Rushworth M: **Social network size affects neural circuits in macaques**. *Science* 2011, **334**:697-700.

37. Bshary R, Oliveira RF: **Cooperation in animals: toward a game**
•• **theory within the framework of social competence**. *Curr. Opin. Behav. Sci.* 2015, **3**:31-37.

This paper proposes that moving forward in the study of evolution and maintenance of cooperation, evolutionary game theory should incorporate the concept of social competence and proximate mechanisms of social behaviour in a holistic framework approach, with flexible and simultaneous games and interacting payoff matrices.

38. Davis V, Holbrook R, Schumacher S, Guilford T, de Perera TB: **Three-dimensional spatial cognition in a benthic fish, *Corydoras aeneus***. *Behav. Processes* 2014, **109**:151-156.

39. Holbrook RI, de Perera TB: **Separate encoding of vertical and horizontal components of space during orientation in fish**. *Anim. Behav.* 2009, **78**:241-245.

40. de Perera TB, Holbrook RI, Davis V: **The representation of three-**
• **dimensional space in fish**. *Front. Behav. Neurosci.* 2016, **10**.

Recent work suggests that the accuracy of three-dimensional spatial representation and the shape of place-cell fields in the brain is defined by the animals' freedom of movement. The results of this study show fish also have a higher order representation of three-dimensional space and are consistent with spherical place fields in fish, thus indicating fish use similar mechanisms to encode space as other vertebrates that move in three dimensions (*e.g.* bats).

41. Healy S, Braithwaite V: **Cognitive ecology: a field of substance?** *Trends Ecol. Evol.* 2000, **15**:22-26.

42. White GE, Brown C: **A comparison of spatial learning and memory capabilities in intertidal gobies**. *Behav. Ecol. Sociobiol.* 2014, **68**:1393-1401.

43. White GE, Brown C: **Cue choice and spatial learning ability are affected by habitat complexity in intertidal gobies**. *Behav. Ecol.* 2016, **2014**:aru178.

44. White GE, Brown C: **Site fidelity and homing behaviour in intertidal fishes**. *Mar. Biol.* 2013, **160**:1365-1372.

45. White GE, Brown C: **Microhabitat use affects brain size and**
• **structure in intertidal gobies**. *Brain Behav. Evol.* 2015, **85**: 107-116.

In this paper, 4 species of gobies from differing habitats are used to test the ecological cognition hypothesis. It appears fish show a trade-off of neural investment in specific brain lobes according to habitat complexity, which seems to be linked to spatial learning and cue use in each habitat.

46. Garamszegi LZ, Eens M: **The evolution of hippocampus volume and brain size in relation to food hoarding in birds**. *Ecol. Lett.* 2004, **7**:1216-1224.

47. Lavenex P, Steele MA, Jacobs LF: **Sex differences, but no seasonal variations in the hippocampus of food-caching squirrels: a stereological study**. *J. Comp. Neurol.* 2000, **425**:152-166.

48. Brown C: **Comparative evolutionary approach to pain**
•• **perception in fishes**. *Anim. Sentience: Interdiscip. J. Anim. Feeling* 2016, **3(5)**.

This is a seminal commentary paper in the debate of fish pain, where the author dismisses Key's (2016) mechanistic and human-centric arguments against fish pain perception using our basic understanding of evolutionary processes

49. Sneddon LU: **Pain in aquatic animals**. *J. Exp. Biol.* 2015,
•• **218**:967-976.

This review combines recent research on nociceptors and pain-related changes in behaviour in fish, as well as some invertebrates, outlining that the neurophysiological basis of pain in fish is demonstrably similar to that in mammals and thus we should accept fish are capable of experiencing pain and consider wider implications of human use of these animals.

50. Rose JD, Arlinghaus R, Cooke SJ, Diggles BK, Sawynok W, Stevens ED, Wynne CDL: **Can fish really feel pain?** *Fish Fish.* 2014, **15**:97-133.

51. Key B: **Why fish do not feel pain**. *Anim. Sentience: Interdiscip. J. Anim. Feeling* 2016, **1**:1.

52. Rey S, Huntingford FA, Boltana S, Vargas R, Knowles TG, Mackenzie S: **Fish can show emotional fever: stress-induced hyperthermia in zebrafish**. *Proceedings of the Royal Society B: The Royal Society* 2015:20152266.

53. Cabanac M, Laberge F: **Fever in goldfish is induced by pyrogens but not by handling**. *Physiol. Behav.* 1998, **63**:377-379.

54. Briese E: **Emotional hyperthermia and performance in humans**. *Physiol. Behav.* 1995, **58**:615-618.

55. Briese E, De Quijada MG: **Colonic temperature of rats during handling**. *Acta Physiol. Lat. Am.* 1969, **20**:97-102.

56. Cabanac M, Gosselin F: **Emotional fever in the lizard *Callopistes maculatus* (Teiidae)**. *Anim. Behav.* 1993, **46**:200-202.

57. Rey S, Digka N, MacKenzie S: **Animal personality relates to thermal preference in wild-type zebrafish, *Danio rerio***. *Zebrafish* 2015, **12**:243-249.

58. Lucon-Xiccato T, Bisazza A: **Discrimination reversal learning reveals greater female behavioural flexibility in guppies**. *Biol. Lett.* 2014, **10**:20140206.

59. Laland KN, Reader SM: **Foraging innovation is inversely related to competitive ability in male but not in female guppies**. *Behav. Ecol.* 1999, **10**:270-274.

60. Cole EF, Quinn JL: **Personality and problem-solving performance explain competitive ability in the wild**. *Proceedings of the Royal Society of London B: Biological Sciences* 2011. rspb20111539.

61. Morand-Ferron J, Cole EF, Rawles JE, Quinn JL: **Who are the innovators? A field experiment with 2 passerine species**. *Behav. Ecol.* 2011, **22**:1241-1248.

62. Graham Kerrie Lewis, Burghardt Gordon M: **Current perspectives on the biological study of play: signs of progress**. *Q. Rev. Biol.* 2010, **85**:393-418.

63. Burghardt GM: **Play in fishes, frogs and reptiles**. *Curr. Biol.* 2015, **25**:R9-R10.

64. Burghardt GM, Dinets V, Murphy JB: **Highly repetitive object play in a cichlid fish (*Tropheus duboisi*)**. *Ethology* 2015, **121**: 38-44.

65. White S, Wagner T, Gowan C, Braithwaite V: **Can personality predict individual differences in brook trout spatial learning ability?** *Behav. Processes* 2016 http://dx.doi.org/10.1016/j.beproc.2016.08.009.

66. Mamuneas D, Spence AJ, Manica A, King AJ: **Bolder stickleback fish make faster decisions, but they are not less accurate**. *Behav. Ecol.* 2015, **26**:91-96.