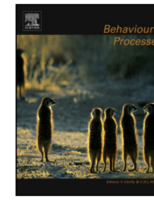
Behavioural Processes 100 (2013) 153–159

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Functional aspects of emotions in fish

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ARTICLE INFO

Article history:
Received 19 March 2013
Received in revised form
10 September 2013
Accepted 11 September 2013

Keywords:
Emotions
Behaviour
Cognition
Psychology
Fish
Evolution

ABSTRACT

There is an ongoing scientific discussion on whether fish have emotions, and if so how they experience them? The discussion has incorporated important areas such as brain anatomy and function, physiological and behavioural responses, and the cognitive abilities that fish possess. Little attention has however, been directed towards what functional aspects emotions ought to have in fish. If fish have emotions – why? The elucidation of this question and an assessment of the scientific evidences of emotions in fish in an evolutionary and functional framework would represent a valuable contribution in the discussion on whether fish are emotional creatures. Here parts of the vast amount of literature from both biology and psychology relating to the scientific field of emotions, animal emotion, and the functional aspects that emotions fulfil in the lives of humans and animals are reviewed. Subsequently, by viewing fish behaviour, physiology and cognitive abilities in the light of this functional framework it is possible to infer what functions emotions may serve in fish. This approach may contribute to the vital running discussion on the subject of emotions in fish. In fact, if it can be substantiated that emotions are likely to serve a function in fish similar to that of other higher vertebrate species, the notion that fish do have emotions will be strengthened.

Contents

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http://dx.doi.org/10.1016/j.beproc.2013.09.002

1. Historical development – human thinking of animal emotion

'Pleasures and pains' or emotions have played a key role in human thinking about animal behaviour throughout the history. Aristotle (384 BC–322 BC) wrote in his book 'History of Animals' that '*all animals pursue pleasure in keeping with their nature*'. The French 17th century philosopher René Descartes has often been blamed for the view that animals are without feelings, but did in fact write about fear, hope and joy as motivating the behaviour of animals (Fraser and Duncan, 1998). Jeremy Bentham, the well known English philosopher and lawyer was one of our first proponents of animal rights. He emphasized that the ability to experience 'pleasures and pains' should be the only criterion essential to hold or deserve an inherent moral status. Bentham is much quoted in animal rights and animal welfare for stating. 'The question is not can they reason? Nor can they talk? But can they suffer?' Bentham's pleasures included those derived from satisfying hunger and thirst, from sexual experiences, from health and from gratifying curiosity. His pains covered feelings arising from disappointment, hunger, thirst, disease or experiencing excessive heat and cold (Bentham, 1823).

Thirty years later Herbert Spencer (1855) put these ideas into a more biological context by proposing that feelings are adaptations. He believed that feelings combined with memory and reason allowed an animal to substitute flexible, adaptive reactions for merely reflexive ones. Nevertheless, the perhaps most influential publication on animal emotion came in 1872 with Charles Darwin's. 'The expression of emotions in man and animals', which will be addressed shortly.

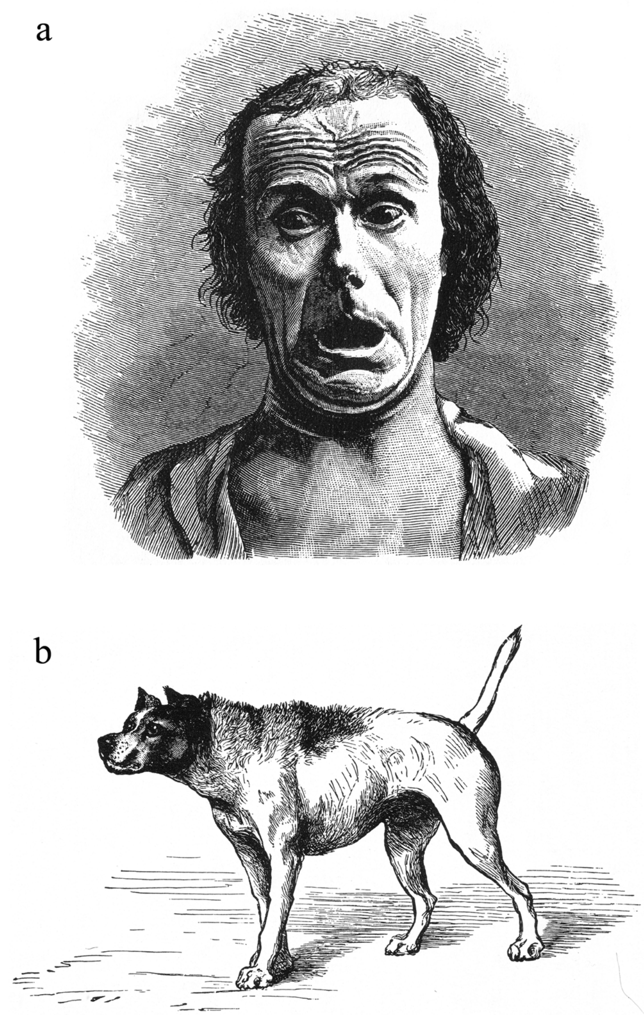

Fig. 1. Drawings depicting emotional expressions in man and dog published in Charles Darwin's book 'The expression of emotions in man and animals' (1872).

1.1. The science of emotion

The science of emotions has been termed both contradictory and confusing. Many models and theories exist, partly because researchers have focused on different components of the emotional reaction such as expressions, behaviour or physiology. A major problem in the field of emotion has been the wide variety of definitions that have been proposed. In an attempt to resolve the resulting confusion, 92 definitions were in 1981 compiled from a variety of sources in the literature of emotion. These definitions were classified into 11 different categories, on the basis of the emotional phenomena or theoretical issues emphasized in the various definitions (Kleinginna and Kleinginna, 1981). This certainly illustrates the complexity of the concept of emotions.

In the present article two examples of how an emotion can be defined are included. These are two quite recent definitions that do operate on different levels but still indicate something essential about emotions. The American psychologist and professor of medicine Robert Pluchik, stated that an emotion is not simply a feeling state. An emotion is a complex chain of events that begins with a stimulus and includes feelings, psychological changes, impulses to action and specific, goal-directed behaviour (Plutchik, 2001). A somewhat simpler but elegant definition was proposed by neuroscientist Jaak Panksepp who defines emotions as 'processes which are likely to have evolved from basic mechanisms that gave animals the ability to avoid harm or punishments and to seek valuable resources or reward' (Panksepp, 1998). It is worth noting that both definitions emphasize goal-directed behaviour and thus the ultimate and adaptive nature of emotions, while the first also includes proximate aspects.

1.2. Traditions within the science of emotion

Different scientific traditions such as the evolutionary, the psycho-physiological and the cognitive perspective have contributed with important developments in the understanding of emotions. From an evolutionary perspective Charles Darwin's publication 'The expression of emotions in man and animals' can be seen as a cornerstone of modern emotion research. The general impact of this publication was that behaviours were seen as functional properties of species that played a significant role in adaptation. Furthermore, emotions were no longer seen as dysfunctional, in the sense as something to reject or control, but instead as something being functional and ultimately essential for survival (Scherer et al., 2001). Darwin also put much emphasis on the social and communicative function of emotions as illustrated by the several drawings depicting animals and human faces experiencing different emotions (Fig. 1). Subsequently, in the wake of Darwin's theory of evolution, it became common to view emotions and other mental states of animals including humans as adaptive products of natural selection.

In the late 19th century a psycho-physiological perspective on emotions was at the centre of attention. Emotions were looked upon as part of a chain with multiple events that prepared the organism for potential action and provided the individual with information regarding the meaning of the current state of the environment (Scherer et al., 2001). A question that received quite a deal of attention is what happens first, the emotion or the physiological arousal?

Encountered a frightening stimulus, psychologist William James, believed that peripheral physiological activation in the body took place first and then was accompanied by the emotion fear; 'We feel afraid because we tremble' (James, 1890). This view of emotion is known as the James–Lange theory. The Cannon–Bard theory on the other hand argues that the emotion arises first in the central nervous system and that the emotion is responsible for initiating the physiological responses. In fact the question was more nuanced, the core difference between Cannon and James boiled down to whether the experience of emotion does or does not require the perception of physiological bodily changes. In fact, this debate has not ended yet (Scherer et al., 2001).

Contrary to some popular notions, emotions do not generally 'get in the way' of rational thinking, emotions are in fact essential to rationality. In the1960s several influential researchers introduced the cognitive aspect into the science of emotion. Schachter and Singer (1962) included cognition in their 'two-factor theory of emotion'. According to this theory cognition were used to interpret the meaning of a physiological activation and also the emotion that aroused (Schachter and Singer, 1962). Cognition has later been defined as 'the mechanism by which animals acquire, process, store and act on information from the environment' (Shettleworth, 2001).

The key factor in the current emerging understanding of emotions has been that emotional reactions are the consequence of some sort of information processing. This processing is now commonly referred to as appraisal (Scherer et al., 2001). The appraisal theory of emotions was originally developed by Arnold who emphasized that appraisal is different from the mere perception of a situation because it involves an estimation of the relevance of the situation, and how it affects the individual and its goals (Arnold, 1969; Scherer et al., 2001). The ability to perceive own emotions enables an individual to detect and assess a discrepancy between its requirements and the environmental conditions. Appraisal can be unconscious and are affected by innate responses as well as experience, learning and memory (Desire et al., 2002; Scherer et al., 2001). A key function of emotions as seen by many scientist are that emotional reactions can be seen as functionally freeing the individual from hard wired and innate responses and allowing more flexible, adaptive responses (Scherer et al., 2001).

Today an emotion may be classically described through a cognitive component, an autonomic component including visceral and endocrine responses, a behavioural component such as a posture or activity and a subjective component – the emotional experience or feeling (Scherer, 2009; Desire et al., 2002). In humans the subjective feeling corresponds to the awareness or the conscious experience of the emotion. Concerning animals, some argue that emotions can only be subjective or felt in animals with consciousness. Others again argue that a subjective feeling is likely to be a fundamental part of the emotional process, and that all animals that show emotions behaviourally and physiologically also experience some sort of subjective feeling (see e.g. Dawkins, 2001).

1.3. Classification of emotions

There has been considerable debate whether an emotion should be classified as a position in a continuum or whether emotions are best identified as distinct states. Some scientists have chosen to see emotions as on a two dimensional scale, where one scale is the arousal or the strength of the emotion and the other represents the valence of the emotion – whether it is positive or negative (see e.g. Russell, 1980; Rolls, 2000) (Fig. 2). Fear is for example considered an emotion with high level of arousal and a highly negative valence, whereas to be content on the other hand, has a low degree of arousal and is found on the positive side of the valence scale.

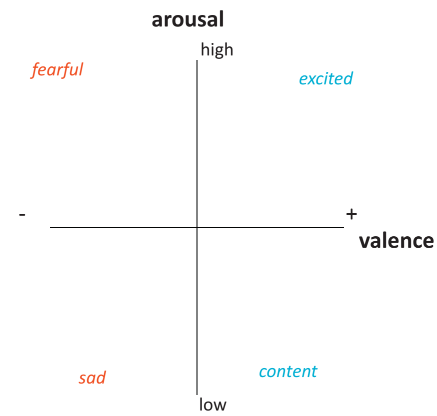

Fig. 2. Emotions portrayed on two dimensions, one representing the degree of arousal, the other the valence of the emotion. Modified from Russell (1980).

Others have classified emotions as separated and specific states with behavioural and physiological correlates (e.g. Ekman, 1992; Plutchik, 2001). This view supports a small number of basic or primary emotions such as for example fear, happiness, sadness, disgust and anger. While more complex emotions such as jealousy, grief, envy, regret and guilt are believed to be mixed states occurring as combinations or mixtures of the primary emotions (Plutchik, 2001).

2. Functional aspects of emotions

The functional aspects of emotions are various. In general emotions enable us to avoid harm and to seek valuable resources (Panksepp, 1998), or as Cabanac has argued 'pleasant is useful' and guides human and non-human animals to perform behaviour that serves to enhance their fitness (Cabanac, 1992). More specifically, psychologist and neuroscientist Edmund Rolls (2000) argues that emotions are highly functional in the following aspects;

- Emotions elicit autonomic and endocrine responses and allow flexibility in behavioural responses.
- Emotions motivate behaviour and are functional in communication and social bonding.
- Emotional processing includes cognitive evaluation of stimuli and is essential in storage and recollection of memories.

There is considerable evidence that events which induce positive or negative emotions, are more readily remembered than those which are emotionally neutral (Paul et al., 2005). This memory enhancing effect is most likely adaptive in that emotionally arousing stimuli, both positive (e.g. sexual, food related) and negative (e.g. predation threat) are more likely to contribute to survival and reproduction than memories from neutral stimuli (Paul et al., 2005).

Plutchik (2001) argued to place emotions in an evolutionary and functional framework and define emotions in terms of what their function might be. He believed that the concept of emotion is applicable to all evolutionary levels and thus relates to animals as well as to humans. Despite the fact that emotions may have different forms of expressions in different species he recognized certain common elements, or prototype patterns that can be identified, followed by generally the reestablishment of an equilibrium state (Table 1). Plutchik supported a view of eight primary emotions and believed that other more complex emotions are a mixture of the primary emotions and occur as combinations of these.For example a confrontation with a threatening stimulus elicits a cognitive evaluation portraying danger and the emotion fear occurs. The associated overt behaviour is to escape and the effect or functional aspect of fear is

Table 1
Associated behaviours and functionality of eight primary emotions. Modified from Plutchik (2001).

Emotion	Associated behaviour	Functional aspect
Fear	Escape	Achieve safety
Anger	Attack	Destroy obstacle
Joy	Retain or repeat	Gain resources
Sadness	Cry	Reattach to lost object
Acceptance	Groom	Mutual support
Disgust	Vomit, avoid	Avoid or eject poisonous food
Expectation	Map, explore	Gain knowledge of new territory
Surprise	Stop	Gain time to orient

thus to reestablish safety. Anger is elicited by an obstacle or enemy, the associated behaviour is to attack and the functionality is thus to destroy an obstacle or remove an enemy. Joy on the other hand is experienced if you gain a valuable object or resource. The function of joy is to retain the resource or even make you repeat whatever you did so that you can gain new resources. Disgust serves the function to avoid poisonous food, while surprise makes you stop to gain time to orient (Plutchik, 2001).

3. Measure animal emotion

In spite of Darwins publication back in 1872 it has taken time to view emotions in a phylogenetic continuity and as a universal phenomena relating to both humans and animals. Especially the development of Behaviourism in the last century contributed in making it unacceptable and anthropomorphic to assign, or even study, emotions in animals, as the behaviourists emphasized merely observable behaviour of animals and humans that could be described scientifically without any recourse to internal processes (Behaviourism, 2013).

However today extensive research, among others on neural circuits in the brain has shown that for example the limbic system concerned with the experience and expression of emotions exist also in animals. As a consequence, the understanding of emotions and their influence and function in animal behaviour and welfare has increased (see e.g. Duncan, 1996; Spruijt et al., 2001; Mendl and Paul, 2004).

It is not possible to know exactly the feelings of any other individual, whatever species (Nagel, 1974; Broom, 1998). To measure animal emotion is especially challenging, as animals cannot tell us how they feel verbally. Therefore when we attempt to approach animal emotion we have to use indirect measures. Physiological parameters such as increased heart rate, elevated blood pressure and the release of adrenalin or cortisol are often used as indicators of emotions. However, physiological parameters may indicate level of arousal but not necessarily valence and therefore they need to be treated cautiously and should idealy be associated with other measures to indicate emotion.

Emotions are thought of as processes that enable animals to avoid danger and harm, and allow them to work towards desirable recourses and reward (Panksepp, 1998). By using behavioural tests we can apply motivation and preferences as indicators of emotions. We can assume that approach towards and/or preferences for an area or object involve some sort of positive emotion. Furthermore, if an animal is willing to work hard to gain access to a resource we can infer that this resource is associated with reward and an especially pleasurable emotion. Avoidance responses on the other hand may reflect a negative emotion such as fear. Furthermore, reduced attention or motivation to perform a certain task might also be reflective of a negative affective state. Hence, we can make predictions about various emotions by observing animal behaviour.

One can also present stimuli of a certain character and thereby try induce a specific emotional state in animals. The emotion fear is for example thought to be elicited by sudden, unpleasant, unfamiliar and unpredictable stimuli (Desire et al., 2002). By presenting stimuli with such characteristics and monitor body language, behaviour and physiology we can gain knowledge of the animal's expressions during that particular emotional state, or put simply 'how fear looks'. By signalling a learned event, either positive or negative, we can also monitor emotional expressions as the animal are anticipating what is to come, and in that way learn about the emotional expressions of different species (see e.g. Moe et al., 2006). While behavioural indicators and emotional expressions are especially valuable in the study of animal emotion it should be mentioned that emotions may also exist without any specific expressions or behavioural change to indicate them (Broom, 1998).

Before I move on to the topic of emotions in fish in particular I would like to return to the functional aspects of emotions briefly. Put simply emotions have to do with avoiding the bad and seeking out the good, and as such, almost all things in life are dependent on some sort of emotional processing. Emotions are highly functional in all the following life-essential tasks (see e.g. Cabanac, 1992; Broom, 1998; Plutchik, 2001);

- Interaction with and exploration of the environment.
- Interaction with conspecifics.
- Avoidance of predators.
- Avoidance of tissue damage.
- Engaging in mating and raise young.
- Avoidance of poisonous objects or food.
- Learning, remember and adjustment of behaviour accordingly.
- Searching, hunting for and ingestion of food.
- Decision-making.

Are these aspects relevant for fish? The evident answer is yes, fish need to fulfil the same functions and perform the same tasks. Simpler vertebrates do adapt to many of the same challenges as higher vertebrate species and have similar socio-ecological challenges in life-history and the environment. What about other premises for emotions, do fish fulfil these?

4. Emotional premises in fish?

It is difficult for humans to see fish as creatures with emotions. They are often spoken of in terms of 'crops' and 'harvesting' in the industry and we most often encounter them when they are flopping helplessly around on the shore or laying very still in the freezer at the supermarket. However, for example divers, aquarium holders and scientists that watch fish hunt for food, engage with mates or raise young most certainly gain a very different view of the behavioural complexities and the life that fish lives (Pitcher, 2006).

It is important to mention that the term 'fish' covers a wide and very disparate group of vertebrates. Only in teleosts, a group of bony fish, there are more than 20 thousand living species that inhabit diverse aquatic environments and thus possess a vast range of specific adaptations and variations. Only a small number of species have been studied in any scientific detail. It is therefore important that generalization across different fish species should be used with some caution (see e.g. Braithwaite et al., 2011).

The scientific debate concerning whether fish have emotions or not have largely focussed on brain anatomy and function, physiological and behavioural responses and the cognitive abilities that fish possess.

4.1. Fish brain anatomy and physiological responses

Fish have marked differences in structures and relative brain size compared to higher vertebrates and some scientist (e.g. Rose, 2002) have argued that since fish lack the neocortex they cannot experience emotions. On the other hand, increasing amounts of scientific evidence suggest that the fish telencephalon has functional homologous limbic and dopaminergic structures involved in emotional processing. For example have recent studies identified structures in the telencephalon that appear to be homologue to the mammalian amygdala and hippocampus. Fish that had these areas lesioned showed alterations in fear responses, spatial learning and memory (Portavella et al., 2004). It appears that emotions do involve relatively primitive brain circuits that have been conserved through vertebrate evolution (Chandroo et al., 2004).

As regards the physiological component of emotions, fish show stress responses largely similar to mammals. Fish release adrenalin and noradrenalin, resulting in increased heart rate and ventilation among others. Fish also produce cortisol in response to emotional stimuli (Bonga, 1997) and there have been identified transmitter substances in fish such as dopamin, seretonin and oxytocin/isotocin that are associated with emotional phenomena like reward and mood in humans (Winberg and Nilsson, 1993; Thompson and Walton, 2004).

Pain has received a substantial amount of attention in the debate concerning fish emotion and several studies have shown that fish do possess important criteria for pain perception. Nociceptors, natural pain-killers (opioids), neural pathways and brain areas for pain processing have all been identified in fish (Braithwaite, 2010; Braithwaite and Boulcott, 2007; Sneddon, 2004; Sneddon et al., 2003a; Broom, 2001).

4.2. Behavioural responses and cognitive abilities in fish

Behaviour is an important window into the mind of animals and thus also their emotions. Emotions do as previously mentioned motivate behaviour and permit more flexible responses (Rolls, 2000). Fish behavioural responses have been investigated in several contexts designed to elicit an emotion.

4.2.1. Fear and pain

Fear serves a function that is fundamental to survival and activates behaviours that protects the animal from threats. Several behavioural responses to threatening stimuli have been described in fish. Furthermore, a number of studies have shown that similar behavioural responses are shown in response to conditioned stimuli. This implies that the displayed behaviours are not merely reflexes, and that cognitive processes occur. For example do both Rainbow trout and Atlantic salmon escape to another compartment of the aquaria when a threat in the form of a plunging dipnet is signalled beforehand by light (Yue et al., 2004; Eriksen, personal communication 2009).

Pain serves the function to protect organisms from damage and pain will generally result in an avoidance response. The behaviours one has observed in fish during or after pain infliction are compatible with the same function (Table 2). Fish do for example show avoidance responses typically starting with a powerful tail-flip (Chervova, 1997; Dunlop et al., 2006; Nordgreen et al., 2009). While such responses can be purely reflexive and functional in limiting damage in an acute situation, it has been shown that fish have the ability to learn to avoid painful stimuli in ways that cannot be explained merely as simple reflexes. Fish can learn to avoid areas and objects previously associated with painful stimuli. For example carpe fish that has been hooked once can be difficult to catch for up till a year afterwards on the same type of bait (Beukema, 1970). Rainbow trout injected with bee venom or acetic acid in the mouth area exhibited anomalous behaviours such as a rocking motion and they were observed rubbing their mouth towards walls in the aquarium allegedly in order to remove or decrease the pain sensation. Furthermore, they showed a reduction in responses towards a previously positive conditioned stimuli, suggesting that pain also affects motivation negatively (Sneddon et al., 2003a,b; Reilly et al., 2008).

Table 2
Behavioural responses observed in fish during or after encountering a painful stimulus.

Behavioural responses in fish during or after pain infliction	References
Tail-flip (avoidance)	Chervova (1997), Dunlop et al. (2006), Nordgreen et al. (2009)
Freezing (avoid further damage)	EFSA (2009)
Avoidance of area	Portavella et al. (2004), Dunlop et al. (2006), Nordgreen et al. (2009)
Avoidance of object	Beukema (1970), Brown (2001)
'Rubbing' (removal) and 'rocking'	Sneddon et al. (2003a), Reilly et al. (2008)

4.2.2. Positive emotions

Positive emotions or positive affective motivational states are functional in that they direct behaviour towards for example eating, mating, playing and exploring (Balcombe, 2009). While the function of eating and mating is fairly evident, playing is thought to be important in social relations among other thing and exploration is purposeful in that it may lead to the acquisition of resources.

As with mammals, there exist few studies investigating positive emotional states in fish. However, a few studies applying learning procedures with positive reinforcement are likely to reflect the behaviour of fish experiencing some sort of positive emotion. Nilsson et al. (2008) used conditioning and trained groups of cod (*Gadus morhua*) to associate a light signal with a positive up-coming event, i.e. the delivery of food. The fish showed anticipatory behaviour and gathered in the feeding area after they had been presented with the light signal. The memory of this association between light and the delivery of food was retained for at least 3 months. It has also recently been shown in cod that environmental enrichment promotes a higher propensity for exploration of novel areas and socially facilitated learning (Strand et al., 2010).

4.3. Consciousness and cognitive complexity in fish

An illustration of cognitive complexity could indicate that animals process information at several mental levels, one of which could be conscious (Paul et al., 2005). Consciousness, when the term is applied to animals, often relates to the capacity to be aware of one's own thoughts, sensations and emotions (Mendl and Paul, 2004). Consciousness has also been defined as the ability to generate a mental scene in which diverse information is integrated for the purpose of directing behaviour of self (Edelman and Tononi, 2000).

A study illustrating the cognitive complexity that some fish possess was done by Oliveira and co-workers (1998). They tested whether male Siamese fighting fish paid particular attention to displays between other males, and whether they used this information in subsequent contests with the males they had observed. Fish that were allowed to watch other fish interact took significantly longer time to approach and longer to display agonistic signals to *seen* winners than to *seen* losers. There was no such difference for *unseen* winners and losers. It is apparent that the fighting fish has the ability to eavesdrop on interactions between other males, and through observational learning remember and actively adjust their own behaviour according to the information they have received (Oliveira et al., 1998).

Trace classical conditioning is the association of stimuli across time gap, and is in humans an indication of awareness and the ability to form declarative representations (Clark and Squire, 1998). Declarative memory is memory of facts and events and thus requires a higher degree of consciousness compared to more procedural memories e.g. motor skills and habits (Squire, 2004). A few very interesting studies has investigated fish's abilities to learn by trace conditioning. Nilsson et al. (2008, 2010) demonstrated that Atlantic cod and Atlantic halibut trained in an appetitive Pavlovian conditioning programme associated stimuli separated by a time gap of one minute. Some individuals showed anticipatory behaviour even with a time gap of two minutes between the conditioned stimulus and the delivery of food (unconditioned stimulus). The Atlantic cod retained the learnt association for at least three months. The same research group also showed that cod could change their interpretation of a fear-inducing dipnet to a signal of a forthcoming reward, when the dipnet was paired with the delivery of food 10 s after exposure (Nilsson et al., 2012).

Trace conditioning has also been studied in a salmonid specie, the rainbow trout. In this study trout were conditioned to expect a food pellet following a green light and the trout started to display an appetitive response to the light. Furthermore the appetitive response of the trout was altered following a devaluation of the unconditioned stimulus (the food pellet) as it was paired with a mild electric shock. The trout displayed flexible behaviour and presumably they used previous experience (light means food, but food means shock) to avoid further electric shocks (Nordgreen et al., 2010).

The question whether animals experience emotions in a conscious way is particularly challenging. While a few scientists believe that the experience of subjective, conscious emotions arouse with the development of language in humans, most are really concerned about to what degree animals consciously experience emotions and which animals to include in such a sentient group. Until quite recently fish have exclusively been disqualified from such a group. Recent studies, like the one illustrating the ability of the Siamese fighting fish to eavesdrop on interactions between other individuals and adjust their behaviour accordingly, and the studies on trace conditioning in fish, reveals that fish possess far more complex cognitive abilities than previously thought. This complexity can be used as an argument that fish also may perceive emotions in a conscious or subjective way. However it remains largely an open question as to whether cognitive complexity is a true indicator of greater capacity for emotional experience (Paul et al., 2005).

4.4. Communication and social bonding in fish?

The functional aspects of emotions include, among other, communication and social bonding (Rolls, 2000). One might argue that more complex emotions like love, acceptance or a feeling of affiliation have evolved with increasingly complex social structure and that fish do not possess such emotions. As to what degree emotions play a part in fish communication and social relationships we know very little, however it is thoroughly documented by now that fish are social and do communicate (see e.g. Heg et al., 2005; Rosenthal and Lobel, 2006). Whether fish communication in its various forms, visual, chemical, auditory or electric contains an emotional component is hard to say, but not a possibility to categorically neglect. An example that speaks of an emotional component at least in certain parts of fish communication is that the release of chemical alarm substances from injured fish provokes behavioural fright reactions in conspecifics of Crucian carp (*Carussius carrussius*) and other fish species (Doving and Lastein, 2009). Moreover, we now know that fighting fish meeting a rival can choose whether or not to display agonistic signals and engage in fights. According to Plutchik (2001) the sight of a rival or enemy may induce the emotion anger, the associated behaviour is attacking and the functional aspect to remove the enemy being an obstacle in your way.

Many fish species have the ability to recognize individuals and some species that are mouth brooders take substantial care of their offspring. Fish from the family Cichlidae have the most highly advanced social system of any fish species known to date. In the breeding season many cichlids form monogamous pairs and have helpers. Both related and unrelated fish of both sexes share in cleaning territory and defending the brood (see e.g. Le Vin et al., 2011). The motivational basis for such behaviour might be emotional. In fact, studies in the zebrafish (*Danio rerio*) have shown that proximity to a conspecific has rewarding properties and that the sight of a conspecific can be used to reinforce behaviour in an associative learning task (Al-Imari and Gerlai, 2008). Possibly does social contact elicit positive emotional states in social fish species? On the other hand are negative feelings, such as loneliness, believed to serve the function to restore social contact if an individual has been separated from its group, at least in other higher vertebrate species (Broom, 1998).

5. Do fish have emotions?

Emotions are adaptive products of natural selection that have played an important part in maximizing fitness throughout history. The principle of phylogenetic continuity suggests that the differences between fish and higher vertebrates in the functional aspects of emotions are rather a matter of degree than of kind. Furthermore, the fact that fish meets many of the same socio-ecological challenges as do other vertebrates supports a similar view. The presented studies on fish illustrate that we can approach and seek to study emotions in fish through at least three of the four classical components in an emotion; the cognitive, the physiological and the behavioural component. The subjective component is difficult to approach in all species, but efforts are being made for example through studying emotionally induced cognitive bias in animals (Mendl et al., 2009; Harding et al., 2004).

If we keep in mind Rolls list of the functional aspects of emotions (2000) and the above mentioned fish studies we recognize that emotions are likely to serve many of the same functions in fish as in other animals including humans. Emotional stimuli elicit autonomic and endocrine responses in fish, they induce flexible behaviour and they motivate behaviour. Studies have also demonstrated that fish evaluate stimuli in a cognitive way and that they can remember for a sufficient amount of time. Emotion and cognition affect each other mutually and emotional processing is essential in storage and recollection of memories. As regards communication and social relations in fish there exists less evidence, but it cannot be ruled out that emotions may have functional aspects also in motivating these behaviours. Thus, increasing amounts of experimental evidence suggest that fish have emotional states that are functional in many of the same aspects as in other higher vertebrates. Which range of emotions fish encompass and how they experience them we do not know. Demonstrations of advanced cognitive abilities may indicate that at least some species of fish are able to perceive emotions in a conscious or subjective way. These are challenging but important areas of future research, especially with regard to increasing awareness of the welfare and humane treatment of fish.

Acknowledgement

I am grateful to Marit Skog Eriksen and Paul Midtlyng for commenting on an earlier version of this manuscript.

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