



70th Birthday Contribution

This is a contribution to the virtual special issue celebrating the 70th birthdays of Paul Hart and Tony Pitcher, long-time collaborators and founding editors of the journal.

The proximate architecture for decision-making in fish

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Abstract

Evolution has since the very beginning resulted in organisms which can sort fitness-related information from noise, evaluate it and respond to it. In animals, the architecture for proximate control of behaviour and physiology has been gradually evolving since before the Cambrian explosion of animal phyla. It integrates many different survival circuits, for example for danger, feeding and reproduction, and operates through reflexes, instincts, homeostatic drives and precursors to human emotions. Although teleost brains differ substantially from the much better understood brains of terrestrial vertebrates, their anatomy, physiology and neurochemistry all point towards a common and malleable architectural template with strong and flexible effects on fish behaviour and elements of personality. We describe the main components of this architecture and its role in fish behaviour from the perspectives of adaptation, evolutionary history and gene pools. Much research is needed, as several of the basic assumptions for architectural control of behaviour and physiology in teleosts are not thoroughly investigated. We think the architecture for behavioural control can be used to change ecosystem models from a bottom-up perspective to also include behaviourally mediated trophic cascades and trait-mediated indirect effects. We also discuss the utility of modelling based on proximate architectural control for fish welfare studies.

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Behavioural control through heuristics

Ever since Darwin (1859), animal behaviour has been studied based on the premise that it has emerged through evolutionary adaptation. For almost a century, quantitative evolutionary ecologists simplified the question of adaptive behaviour to the much easier question of optimal behaviour. They used optimization methods to predict the organism's responses to environmental factors (Lotka 1925; Fisher 1930) but without considering constraints. However, while modelled organisms may consider all relevant environmental and physiological information and find the behaviour that most likely will contribute maximally to future reproduction, natural organisms are limited by imperfect information, imperfect ability to analyse it, imperfect ability to foresee consequences of the alternative behavioural options, as well as time constraints.

Rather than making perfect decisions, animals use rules which are learned by experience or evolved by natural selection. These rules are called heuristics. Basically, there are a few types of learning in nature. The most modern is to learn from teachers or from watching others, which may require substantial sensory and cognitive machinery. An older way is to learn from own experience, which requires memory. The oldest way to generate heuristics involves the lineage and is genetic adaptation by natural selection, through which instincts and fixed responses have evolved so that individuals in later generations will behave adequately already at their first exposure to many risks and opportunities. The word learning is not used for genetic adaptation but in principle it is the same that happens, just on a different time-scale and with a different mechanism. The utility of these mechanisms depends among other factors on the types of variability in the environment (McNamara and Houston 1985) and the life expectancy of the organism (Eliassen *et al.* 2007).

Heuristic mechanisms that make quick decisions based on few proximate stimuli have therefore evolved to guide behaviour. Such 'rules of thumb' perform well in a variety of situations (Braithwaite *et al.* 2013; Packard and Delafield-Butt 2014; Eliassen *et al.* 2016), including those never encountered by the organism (Hutchinson and Gigerenzer 2005), and include reflexes, homeostatic drives, instincts and precursors to what evolved into emotions. Below, we will argue that

also in fish, these decision-making processes follow a common and flexible architecture (Fig. 1):

1. an array of sensory cues are monitored to alert of tasks that need prioritization (e.g. feeding, escaping or migrating),
2. the most dominant one will determine a global organismic state (e.g. hunger, defence or homing),
3. the individual then restricts its attention to the stimuli that best will address that task,
4. this allows it to arrive at a decision more efficiently using a narrower subset of the most relevant information.

To save energy and time and to perform well, the heuristic mechanisms must be structured. Structured heuristics have been termed 'choice architecture' in medicine (Johnson and Goldstein 2003) and 'decision architecture' in economics (Koh 2005). For animal behaviour, Eliassen *et al.* (2016) introduced 'the proximate architecture for decision-making', to emphasize that this architecture represents the connections between many different types of sensory information used by the organism (including internal signals on physiological and developmental state) and results in behavioural as well as physiological responses that have evolved because of their positive effects on fitness. The proximate architecture for decision-making as described in Eliassen *et al.* (2016) is a generalization of the qualitative architecture of danger avoidance in LeDoux (2012a, 2015). Another proposed proximate architecture is Warburton and Hughes (2011)'s conceptual model of feeding in fish. The most important differences between Eliassen *et al.* (2016) and these other two architectures are that the proximate architecture for decision-making is quantitative (i.e. based on equations that can be used in simulations) and generalized towards different and conflicting challenges. However, many effects, including learning, have not been implemented; in these respects, the verbal Warburton and Hughes (2011) model is more developed.

The architecture that underlies behavioural decisions is built on some of the core architectural elements of the organism, such as the conserved processes for storing and copying genetic information, and the weak regulatory linkage system that allowed fast adaptive evolution in multicellular eukaryotes (Gerhart and Kirschner 2007). The proximate architecture can be seen as an extension of the weak regulatory linkage system to the

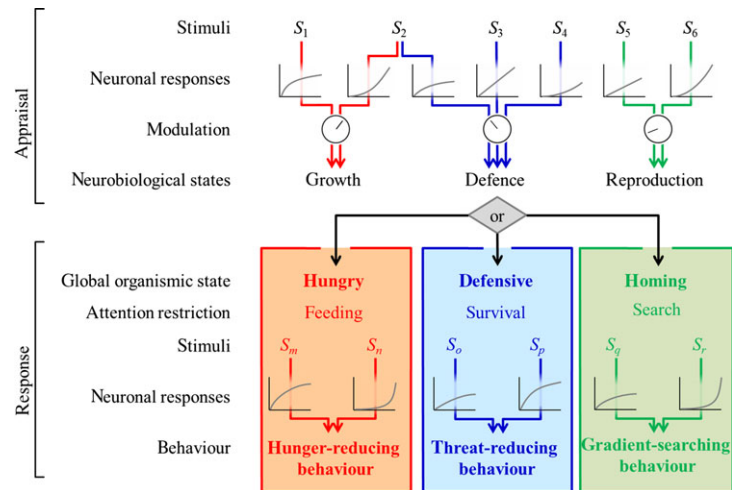


Figure 1 A generalized example of the proximate architecture for decision-making through the integration of survival circuits. The brain can hold several neurobiological states simultaneously (here three shown). The strengths of these depend on the strength of one or more information types S_i (from the body, e.g. stomach fullness or from hormones, or from the external environment, e.g. behaviour of conspecifics) that via neuronal response functions Equation (1) feed into them. Each neuronal response function answers to only one signal, but the same signal can feed into several functions, as illustrated with S_2 . This could for instance be conspecifics, as seeing conspecifics nearby may reduce the stress evoked by a predator while feeding conspecifics may stimulate appetite. The shape of each neuronal response function may vary in the population as it is determined by two genes (see Fig. 2 for explanation to these small neuronal response diagrams). The signals from the neuronal responses may also be strengthened or weakened by modulatory processes (as indicated by the three gauges), for example related to gender, developmental stage, physiological state, learning and memory. However, modulatory processes can potentially have effect anywhere in the figure. The neurobiological states compete, where the stronger determines the global organismic state. In this state, the attention of the organism focusses on making the best available physiological and behavioural response. Modified from Giske *et al.* (2013).

behavioural timescale. While the ultimate evolutionary drives for behaviour are well understood, the proximate drives are less studied, and seldom are the two perspectives combined. When developing the Euler–Lotka equation for optimal animal behaviour, Alfred Lotka commented that ‘What guides a human being, for example in the selection of his activities, are his tastes, his desires, his pleasures and pains, actual or prospective’ (Lotka 1925, p. 352). This is even more relevant for species with more restricted cognitive abilities.

Phylogeny of the underlying infrastructure: brains and neurochemistry

The aim of this section is to show that there is continuity in the adaptive evolution of the control of decision processes from very early animals to mammals and that behavioural control in teleosts can be understood from this perspective.

When Darwin (1872) sought to understand behaviour and its phenotypic manifestations, he turned to emotions. The concept of emotion was

first described from human experience, just as reflexes and homeostatic drives (e.g. hunger and sleep) also are best studied in our own species, while instincts (Lorentz 1950; Tinbergen 1951) more often are assigned to non-human animals. It is difficult to understand how human phenomena such as thirst, hunger, pleasure and fear are experienced by non-humans. Still, these phenomena in the human brain must have originated from earlier and more basic stimulus–response systems (LeDoux 2012a). Several lines of investigation indicate deep evolutionary roots in the architectural design of information processing and the immediate behavioural and physiological responses in mammals and fishes.

Terms used to describe regulation of physiology and behaviour in humans, such as appetite, hunger, stress, anxiety and fear, are relevant across many other animal phyla. When comparing taxa, we could define specific terms for each taxon or accept that the same terms may have somewhat different meanings throughout the tree of life. Another alternative is to use general terms, but

avoid much-used words which describe the human condition in everyday language, as these words are vaguely defined for scientific inquiry (LeDoux 2015). We have chosen the latter option, whenever possible, and we emphasize that when using terms such as 'hunger' and 'decision', we do not imply any mental awareness in the organism. We follow LeDoux (2012a, 2015) in defining a *survival circuit* as a process from sensory information to instrumental behavioural and physiological responses; it is thus a system for organizing the sensing and processing of information and the consequent organismal response to it. Within this process, there are alternative 'neurobiological states' that compete for the short-term control of the organism. We call the resulting activated bodily state of, for example, hunger or predator threat the 'global organismic state' (LeDoux 2012a). Stating that a fish is 'frightened' is shorthand for saying that its coordinated system linking sensory information of threats to decisions activates defensive behaviours aimed at reducing the perceived threat. We do not imply that fish experience these internal states in similar ways to humans. Even in our own species, the inner representation of sensory signals differs among individuals (Humphrey 2006), and it is beyond the scope of this article to discuss whether what humans experience as mental awareness, self-awareness, feelings or emotions, have counterparts in other animals. With these caveats in mind, we dare use some terms of anthropocentric origin to signify classes of natural phenomena as they have been studied in a broad range of species.

Neurochemical similarities have been used to compare mental capacities among different species (O'Connell and Hofmann 2011). Dopamine, serotonin and opioids are associated with survival circuits in humans and are highly conserved in evolution, also in invertebrates (Mustard *et al.* 2005; Kass-Simon and Pierobon 2007; Iliadi 2009; Curran and Chalasani 2012). These molecules are used in reward systems in the brain and function to modify behaviour through learning. The synaptic proteins, allowing rapid behavioural responses, may have existed and been conserved since the dawn of metazoans or before (Burkhardt 2015; Moran *et al.* 2015).

Fish brains produce many of the substances associated with the mammalian behavioural regulation, including dopamine, serotonin and oxytocin/isotocin (Winberg and Nilsson 1993; Bonga

1997; Thompson and Walton 2004; Tognoli *et al.* 2010; Kittilsen 2013; Sørensen *et al.* 2013). The behavioural and physiological effects of treating fish with drugs that affect behaviour in mammals are so similar that Maximino and Herculano (2010) found zebrafish (*Danio rerio*, Cyprinidae) suitable as model organism for neuropsychopharmacological effects of drugs on motivation, emotion and cognition in vertebrates generally. A recent study, testing the rewarding effects of the drug amphetamine, further suggested that the function of the amygdala in emotion in mammals is conserved throughout vertebrate evolution although located in other brain regions (von Trotha *et al.* 2014). Not all drugs reveal the same, strong similarity (Sackerman *et al.* 2010), but a meta-analysis concluded that for substances acting on the serotonergic system (relating to defensive behaviour, such as fear and anxiety in humans), the effects on behaviour were similar in mammals and fish (Lillesaar 2011).

The deep evolutionary roots of behavioural architecture can be traced by comparing three branches of the animal tree of life: the molluscs, arthropods and vertebrates. Experiments have revealed a cognitive bias in honeybees (*Apis mellifera*, Apidae), which under dangerous conditions displayed a bias which is characteristic of depressed and anxious humans (Bateson *et al.* 2011). A similar study on Atlantic salmon (*Salmo salar*, Salmonidae) also demonstrated cognitive biases (Vindas *et al.* 2012). In the squid *Doryteuthis pealeii* (Loliginidae), nociception triggered a change in neurophysiological state and instrumental behaviour: a minor injury triggered a sensitized state with defensive responses (Crook *et al.* 2011, 2013) and increased attention towards predators (Crook *et al.* 2014). These biases and sensitized states indicate that these fish and invertebrates have global organismic states with attention restriction (Mendl *et al.* 2011) which is central in our behavioural architecture model (Fig. 1). The brains of most invertebrates are tiny compared to those of vertebrates, but recent studies show that the cognitive abilities of some insects and other arthropods go beyond what was previously acknowledged (Giurfa 2013). This includes highly contingent integration of multiple sensory inputs in the crab *Heterozius rotundifrons* (Bellidiidae) (Hazlett and McLay 2000), anxiety-like behaviour in the crayfish *Proclanbarus clarkii* (Cambaridae) (Fossat *et al.* 2014), attention direction by fruit flies (*Drosophila melanogaster*,

Drosophilidae) (van Swinderen and Greenspan 2003), application of general rules to new situations by honeybees (Srinivasan 2010) and trade-offs between speed and accuracy in vision of bumblebees *Bombus terrestris* (Apidae) (Dyer 2012). While these examples may suggest sophisticated cognitive processes (Shettleworth 2009), they do not assume conscious emotions, but describe behavioural and physiological changes due to the possession of survival circuit architecture (Paul *et al.* 2005; Mendl *et al.* 2009).

Thus, molluscs, arthropods and vertebrates display central components of survival circuit architecture: the same neuromodulators, brain states and a cognitive bias. The last shared ancestor of these three evolutionary lineages, the flatworm-like last common protostome–deuterostome ancestor nicknamed Urbilateria (Erwin 2005; Bailly *et al.* 2013), or an even older animal, may therefore have possessed an early version of this system. The divergence of these lineages likely started in the very early Cambrian about 543 million years ago, based on conservation of developmental regulatory principles and palaeontological evidence (Erwin and Davidson 2002). However, this does not mean that the system operates similarly in these lineages.

Brain anatomy has changed profoundly during vertebrate evolution. The size and structure of the brains of amniotes (reptiles, birds and mammals) and fish are very different (Kotrschal *et al.* 1998). There is an ongoing discussion as to whether and which parts of fish brains are homologous to parts of the mammalian brain thought to be associated with behavioural control and survival circuits (Mok and Munro 1998). One problem with identifying homologous brain structures between mammals and fish is that their telencephalic development happens through inversion and eversion, respectively. This places similar structures in different locations in the adult brain (Yamamoto *et al.* 2007; Maximino *et al.* 2013). An example of this is the mammalian amygdala, which is strongly involved in the emotion (LeDoux 2000, 2003) and reward systems in the human brain (Parkinson *et al.* 2001; Paton *et al.* 2006; Bermudez *et al.* 2012). Although different views exist (Jesuthasan 2012), evidence reviewed by Portavella *et al.* (2004), Demski (2013) and Maximino *et al.* (2013) points towards the teleost ventral subpallium and the dorsomedial pallium being homologous structures to the mammalian basolateral and central amygdala, respectively.

These are mammalian structures involved in defence and stress responses and expression of instinctive and anxiety-like behaviour (Cheng *et al.* 2014; Silva *et al.* 2015).

In sum, we see a very long continuation of basic elements in functionality, neurobiological states and behavioural control architecture (Salas *et al.* 2006; Brown 2015), but also significant differences in brain structure. While the basic proximate architectural elements in the control of behaviour may have been in place half a billion years ago, the ability to process information has changed profoundly, also within amniotes and mammals (Humphrey 2006).

From information to decision: the proximate architecture for decision-making

The proximate architecture for decision-making (Eliassen *et al.* 2016) illustrates the connectedness as well as flexibility in the pathways from sensing to reaction in animals. The architecture incorporates both motivated and non-motivated behaviour (Eliassen *et al.* 2016); here, the presentation is limited to motivated behaviour with examples from homeostatic drives, precursors to emotions and instincts (Fig. 1). The proximate architecture has two phases and four main components (LeDoux 2000, 2012a,b, 2014; Giske *et al.* 2013; Eliassen *et al.* 2016). In the *appraisal phase*, the global organismic state (GOS) is determined based on sensory information, physiological and developmental state, and motivations. In the *response phase*, the instrumental physiological and behavioural responses are determined and executed. The main component, the *survival circuit* (LeDoux 2012a), links a given type of perception with a relevant response. It is an important factor that contributes to activating the GOS and serves an adaptive purpose by restricting attention and arousing the relevant parts of the brain and body (LeDoux 2012a). There exist survival circuits for all basic life-sustaining mechanisms, and they may have been the evolutionary precursors of the integration of the behavioural architecture (LeDoux 2012a, 2015). Some of these are feeding, thermoregulation and reproduction (LeDoux 2014). The fastest are reflexes which are executed without evoking a brain state. Survival circuits, as most other neurological mechanisms, are most widely studied in mammals, where they are highly conserved between species (LeDoux 2000).

In Fig. 1, we show a simplified example where a homeostatic drive (hunger), a teleost precursor of an emotion (threat response) and an instinct (homing) are three survival circuits that are weighted against each other. In this example, the competition in the brain between vigilance and hunger for control of the phenotype is driven by short-term variation in sensory information, while the onset of life cycle migrations typically is linked to hormones, which again can be produced as a consequence of sensory stimuli (Bauer *et al.* 2011). For example, the shift from feeding to homing in sockeye salmon (*Oncorhynchus nerka*, Salmonidae) is linked to hormones involved in the onset of gonadal maturation (Hinch *et al.* 2006). However, also when the organism is hormone-driven, as in homing, homeostatic drives and threat responses can for the short term take control of the phenotype. Figure 1 can be expanded to include several other attention seeking processes, for example social aggression (territoriality, dominance), sociality, curiosity, resting and mating. The *global organismic state* is determined by the currently strongest of the competing alternative neurobiological states, and again determines the *attention restriction* towards the current challenge. Throughout life, *modulatory systems* may up- or downregulate priorities depending on, for example reproductive state or hormones.

The *global organismic state* (GOS) describes not only the strongest neurobiological state and the directed attention of the brain, but emphasizes that the whole organism may be affected, including neurons, hormones, heartbeat frequency, ventilation, muscle tension, etc. (LeDoux 2012a). In this state, the individual allocates its brainpower and also other physiological resources towards a specific challenge or opportunity. As the GOS also contains a physiological response, it can in some occasions be observed non-invasively (e.g. Höjesjö *et al.* 1999, 2015). By entering a GOS, attention towards relevant stimuli is enhanced while other less relevant stimuli are more or less ignored (LeDoux 2012a). Lower feeding efficiency (Lastein *et al.* 2008) and better chances of survival when threatened (Braithwaite and Boulcott 2007; Ashley *et al.* 2009) can be explained by restricted attention, as can the ceasing of feeding during homing migrations (Kadri *et al.* 1995).

Attention restriction (Mendl 1999; Tombu *et al.* 2011) is a fundamental difference between behaviour based on optimization vs. the idea of architecture for behavioural control. While 'optimal'

agents will consider all behavioural options and select the one that most likely maximizes lifetime reproductive success (Lotka 1925; Fisher 1930), attention restriction in the current global organismic state makes the organism focus on a short-term motive to, for example, reduce its hunger, survive a threat or defend its territory (Lastein *et al.* 2008; Ashley *et al.* 2009; Lau *et al.* 2011; Warburton and Hughes 2011). Attention towards predators and prey are key components of survival and will most definitely be evaluated differently (or ignored) when in different contexts with different goals (Purser and Radford 2011).

Teleosts evaluate predation risk differently when either injured (Braithwaite and Boulcott 2007; Ashley *et al.* 2009) or in a specific reproductive stage (Lastein *et al.* 2008), indicating the effect of focussed attention in the response phase. Males of the two-spotted goby (*Gobiusculus flavescens*, Gobiidae) may experience an attention trade-off between mating behaviour and predation risk (Magnhagen 1991) and gravid three-spine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae) differ significantly from non-gravid females in their antipredator behaviour (Frommen *et al.* 2009).

Although the GOS involves some attention restriction, the switch of focus may be more gradual than what is indicated in Fig. 1. A classic example of graded attention is the preference of starved three-spine sticklebacks to feed in dense swarms of *Daphnia*, while they switched to areas with lower food density when more satiated (Heller and Milinski 1979). This was ascribed to a 'confusion effect', that is that sticklebacks pay an attention cost when eating fast and mentally focussed in a dense patch of swarming *Daphnia*, while this cost is lower outside the patch (Milinski and Heller 1978). Also, when starved three-spine sticklebacks had seen the silhouette of a predatory bird, they chose to eat in the low *Daphnia* densities already from the start of the feeding experiment (Milinski 1984). These experiments can be interpreted as the stickleback maintains a brain state of hunger while being alert to predators (as the neurobiological states at the end of the appraisal phase of Fig. 1), and that its behaviour balances these GOS through a gradual regulation of attention towards prey and predators (Milinski 1985a). From the experiments, the strength of the neurobiological state determining the GOS in sticklebacks seems to impact the degree of attention restriction, so that the 'OR' in Fig. 1 in some cases should be an 'AND'.

Modulatory systems temporarily favour or suppress some global organismic states over others. In the model of Giske *et al.* (2013), the modulatory system may upscale or downscale some survival circuits throughout ontogeny from egg to adult, similar to changing life-history priorities (Giske and Aksnes 1992; Brown *et al.* 2007; Conrad *et al.* 2011). However, many other modulatory systems may be at work. Manipulations of the neurobiological states and GOS by parasites (Barber *et al.* 2000; Barber and Dingemanse 2010) occur at a similar timescale as developmental processes, for instance by increasing (Milinski 1985b; Wilson *et al.* 1993) or decreasing (Giles 1983; Øverli *et al.* 2001; Shaw *et al.* 2009) the strength of anti-predator responses. On a shorter timescale, memory of a frightening event (Lehtiniemi 2005) or of a situation causing skin damage (Sneddon *et al.* 2003; Braithwaite *et al.* 2013) may override new perceptions and maintain the GOS. Learning is a way to improve the decision architecture from experiences, and can modify any part of Fig. 1. On the longest timescale are genetic dispositions, which may be seen as constant or lifelong modulations. In the model of Giske *et al.* (2013), these are represented as genes in the neuronal response functions and the developmental modulatory system, thus allowing lifelong and heritable variation among individuals.

This approach can be extended by genetic linkages, where individuals inherit ‘chromosomes’ with coupled and coevolved genes (Eliassen *et al.* 2016), or by genes with hormonal modulatory impacts, for instance linking metabolic rate, food demand and aggression, or metabolic rate and risk willingness (Houston 2010; Reale *et al.* 2010).

Neuronal response functions convert the strength of each sensory stimulus into signals that can be compared in the fish brain when evaluating which GOS to enter or which action to decide on (Fig. 2). In the model of Giske *et al.* (2013), the neuronal response R depends on the strength of the stimulus S , and is modulated by two individual factors (x and y) which are coded as heritable ‘genes’ and passed on to offspring:

$$R = \frac{(S/y)^x}{1 + (S/y)^x} \quad (1)$$

This sigmoidal function allows for graded responses to weak signals and saturation of strong stimuli (Aksnes and Utne 1997; Ashley *et al.*

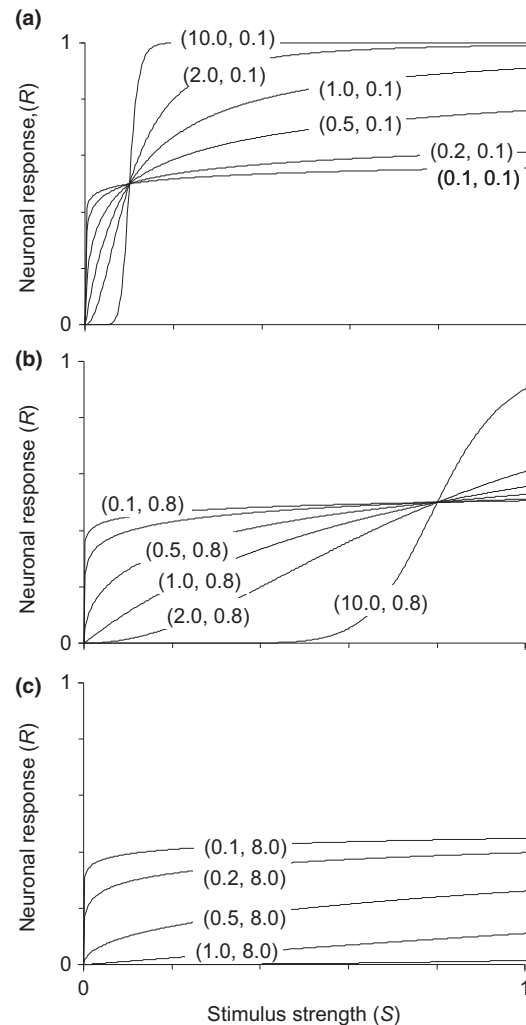


Figure 2 The neuronal response: the graph of Equation (1) for (a) $y = 0.1$, (b) $y = 0.8$ and (c) $y = 8.0$. An individual will in the Giske *et al.* (2013) model have inherited a set of x, y genes for each of its neuronal responses (Fig. 1). Each curve is defined by the x, y gene pair and the stimulus strength Equation (1). The allele of the y gene defines which stimulus strength S gives the neuronal response $R = 0.5$ ($R = 0.5$ when $S = y$), as seen where all lines meet in (a) and (b). As alleles can take values up to 10 while S is scaled up to 1 (see text), high values of y mean that the response will always be weak, as seen in (c). The allele of the x gene determines how sharply the neuronal response increases with S when $S \approx y$, which is best seen in (a). In (c), the curve for $(x, y) = (2, 8)$ is merely visible while the curve for $(10, 8)$ is not visibly different from zero.

2007). Giske *et al.* (2013) scaled each type of sensory signal into the 0–1 range against the maximum ‘observed’ by any fish in the past 50 generations, and limited allele values of the two

genes to the 0.01–10 range. With these definitions, the graph can take many different shapes while always keeping the neuronal response in the 0–1 range, and stronger signals will never give weaker responses (i.e. all neuronal responses are monotonically increasing functions; Fig. 2).

A clear benefit of this approach is the intuitive biological interpretation of how the organism evaluates a sensory signal (Fig. 2). The two genes have functional interpretations, as the y gene defines the S -value where the neuronal response is 0.5 (and most sensitive to changes in the signal strength), and the x gene determines the steepness of the curve around $S = y$. More complex relationships between signal strength and neuronal response can be achieved by adding several independent responses into a complex neuronal response (Andersen 2014; Eliassen *et al.* 2016).

Fish personalities?

The model of proximate architectural control of physiology and behaviour (Fig. 1) explains some of the major factors that may allow consistent individual variation to emerge. Individual differences in behaviour which are consistent over time and situations are referred to as a temperament (Budaev 1997b), coping style (Koolhaas *et al.* 1999), behavioural syndrome (Sih *et al.* 2004) and animal personality (Dingemanse *et al.* 2010; Budaev and Brown 2011). While these concepts are not equivalent and are used somewhat inconsistently in the literature (Stamps and Groothuis 2010; Wolf and Weissing 2012; Mittelbach *et al.* 2014), they point to existent behavioural variability that can be ascribed to individual consistency. Such variation within a population has also been observed in fish (e.g. Budaev 1997a,b; Hart and Salvanes 2000; Ward *et al.* 2004; Webster *et al.* 2007, 2009; Sørensen *et al.* 2013). Many types of personality variation, regardless of whether they originate from genetic factors or from individual experiences, may limit behavioural plasticity and hence prevent behaviour from being optimal (Conrad *et al.* 2011). The proximate architecture gives four perspectives on personality that are worth considering:

1. Variation can exist on different scales: the life-lasting genotype [e.g. variations in metabolic rate (Houston 2010) or the pace-of-life syndrome (Reale *et al.* 2010)], the developing

phenotype with its modulatory systems and the current physiological state (Wolf and Weissing 2010), and due to parasite load (Barber and Dingemanse 2010; Kortet *et al.* 2010; Kekalainen *et al.* 2014). Also habituation and learning may impact coping styles (Fawcett *et al.* 2013; Salvanes *et al.* 2013; Manuel *et al.* 2015), where the genetic disposition for ability to change will depend on life history (Eliassen *et al.* 2007).

2. The proximate architecture (Fig. 1) will in itself open for both genotypic and personality diversity through individual variation in the pathways to decisions (Giske *et al.* 2014). For instance, if the best GOS in a particular situation would be food-searching rather than vigilance, this can come about through weaker emphasis on stimuli related to danger (through neuronal responses or modulatory mechanisms), or by stronger emphasis on stimuli related to feeding. Even for the regulation of feeding, there are many pathways which may vary among individuals or species in importance, such as appetite hormones, emphasis on stomach fullness, on food availability or on social feeding signals.
3. The architecture of the genome also impacts the potential for personality variation. Consider an organism with genes that are not organized on chromosomes, and a reproductive process which randomly delivers the copy of the gene it got from its mother or father to the offspring. Evolution would then preserve those alleles that can contribute to viable offspring when combined with any other allele combination in the gene pool. If on the other hand personality-related genes (such as in the pathway example in the paragraph above) are located close to each other on one or a few chromosomes, evolution of personalities is possible as selection may occur at the level of chromosomes or recombination hotspots (Lichten and Goldman 1995).
4. Considering the combined impacts of genes, physiological state, modulatory systems, habituation and learning, it is likely that what some authors describe as distinct personalities are parts of a continuum in the population. For example, Giske *et al.* (2013) found a difference in one gene in one neuronal response function (the evaluation of conspecifics during feeding competition) to be key for individual variation in the social/solitary axis. This led 'social'

individuals to feed in areas with high concentrations of both food and competitors, while 'solitary' individuals avoided competitors when hungry. Yet there was considerable spatial overlap between these genotypes. Further, these differences were context dependent (Webster *et al.* 2007), as all were 'social' when frightened. In the bold/shy axis, there was continuous variation from predominantly 'bold' to quite 'shy' individuals, with the bulk of the population at intermediate levels (Giske *et al.* 2014).

Can we model fish welfare? There has been a substantial increase in the interest for fish welfare over the past decades (Needham and Lehman 1991; Chandroo *et al.* 2004; Branson 2008; Braithwaite 2010; Turnbull and Huntingford 2012; Kittilsen 2013; Malafoglia *et al.* 2013; Braithwaite and Ebbesson 2014; Brown 2015; Key 2015). Discussions of farmed animal welfare are strongly influenced by the five freedoms outlined in the Brambell Report, which includes freedoms from pain, discomfort and fear, and the freedom to express normal behaviour (Brambell 1965). Research conducted with the purpose of increasing the welfare of farmed or captured fish will often to some degree compromise these freedoms during the experiment. If mathematical models can replace some of the laboratory experiments, unnecessary stress may be avoided and the research process speeded up.

The proximate architecture approach has the capacity to investigate many factors impacting the five freedoms. Behaviours and internal states are used as indicators of fish welfare (Martins *et al.* 2012), for example avoidance behaviour as an indicator of negative welfare and feed intake as an indicator of positive welfare (Huntingford *et al.* 2006). However, our architectural model is yet not ready for this level of precision. For one thing, Fig. 1 does not include memory and learning. Further, as well-being is not a goal in itself for evolution, it is harder to model than life history and behaviour: we do not know what to expect. At the present stage, the model does not converge on the level of defensive behaviour in populations: repeated simulations in the Giske *et al.* (2013) model of fish populations living and evolving in the same environment ended up with very similar life histories and behaviours, but with substantial variation in the tendency to search for food or shelter, and widely differing gene pools (Andersen

2014; Giske *et al.* 2014; Eliassen *et al.* 2016). Maybe this is realistic, given the freedom of the architecture, but maybe the architecture in natural fish is not so free, after all. This variation indicates on the one hand that there are several equally good adaptive outcomes to the use of the two global organismic states investigated (feeding and defence), but on the other hand that the Giske *et al.* (2013) model in its current version cannot predict brain states in a natural fish population. Natural fish have many more global organismic states than these two, and both to include more of them and to differentiate clearly the outcomes of each of them, will likely improve its predictive value. It is also possible that any realistic behavioural architecture gives a freedom for natural selection to determine which pathways are common and dominant and which are less important, as observed in biochemical and cellular architectures (Wagner 2011).

Higher precision modelling of welfare will rely both on a close interaction between further model development and experiments. As the physiological response differs between global organismic states, it is probably a suitable meeting point between model and experiment. Changes in heart rate and ventilation rate following a threat (Höjesjö *et al.* 1999) or a stressor (Bell *et al.* 2010; Barreto and Volpato 2011) can be monitored non-invasively (Altimiras and Larsen 2000), but also through hormonal changes, such as in cortisol levels in response to alarm cues (Carretero Sanches *et al.* 2015). Tailoring the model to fit a specific system will also reduce the pathway freedom in the appraisal phase earlier discussed as a modelling problem. Instead, we can investigate which signals that actually invoke a change in GOS (Carretero Sanches *et al.* 2015; Höjesjö *et al.* 2015). We hope this model approach can stimulate experiments, which then will inform model development to further refine hypotheses, which again are tested, and so on.

Behavioural control in ocean modelling

Proximate architecture is not only relevant for modelling a few individuals in aquaculture. As ecological modelling has gradually become a tool for studying populations and ecosystems, it can be used to explore management issues in fisheries and aquatic ecosystems. It has not been trivial to include plankton or fish behaviour in dynamic

models based in oceanography and lower trophic levels (Giske *et al.* 1998; Carlotti *et al.* 2000; Railsback and Harvey 2013). Ecosystem models have traditionally been in the bottom-up tradition in ecology, where individual growth is assumed to be resource dependent. Behaviourally mediated trophic cascades (Schmitz *et al.* 1997, 2004; Preisser *et al.* 2005; Heithaus *et al.* 2008) and trait-mediated indirect effects (Peacor and Werner 2001) provide different perspectives, whereby the effects of individual risk-sensitive behaviour on both growth and survival are included. It is also interesting in this context that methods are being developed for the study of consistent individual variation even in zooplankton (Ekvall *et al.* 2013; Hylander *et al.* 2014).

Modelling trait-mediated effects requires trait-based models, which again opens for proximate architectures. The spatially explicit physical–biological model for the Norwegian Sea (NORWECOM), which includes biogeochemical modelling of nutrients and phytoplankton, has been expanded with an individual-based module of the copepod *Calanus finmarchicus* (Calanidae) (Hjøllo *et al.* 2012). Modelling of fish also requires horizontal migration, and the first versions are implemented (Utne and Huse 2012). Both the zooplankton and fish modules in the end-to-end ecosystem model (NORWECOM.E2E) are based on evolving suitable parameters through a genetic algorithm (Huse and Giske 1998; Strand *et al.* 2002; Hamblin 2013). The spatially implicit Atlantic salmon population model IBSEM (Castellani *et al.* 2015) also evolves a solution through inheritance and selection in a population. The architectural approach is very suitable for inclusion in such models, as it mimics the natural behavioural process in fish based on local information. While the gradual evolutionary adaptation in the architectural models of Giske *et al.* (2013, 2014) and Eliassen *et al.* (2016) continued for thousands of generations, the evolutionary process was by far the fastest within the first hundred generations. Similarly, an ecologically relevant level of genetic adaptation of parameters in both the NORWECOM.E2E and IBSEM was obtained over merely 10 generations (Utne and Huse 2012; Castellani *et al.* 2015).

Perspectives

The architectural perspective (Fig. 1) gives us two immediate benefits which may seem contradictory:

it makes the simultaneous consideration of a multitude of impacts on behaviour possible, but also gives arguments for the study of one factor at a time. The full scheme can be utilized in evolutionary individual-based modelling (Eliassen *et al.* 2016) as well as in end-to-end ecosystem models, while the GOS and the subsequent attention restriction allow one to experimentally attribute signals to motivations, and motivation to behaviours. In the longer perspective, the survival circuit concept (LeDoux 2012a, 2015) may change how we think about the environment in animal behaviour. ‘The ecology of fear’ is already used to explain why animals do not utilize high-quality patches, even when there are no predators around (Brown *et al.* 1999). The same goes for light avoidance in fish (Giske and Salvanes 1995), but also for much more. As the experience of the environment depends on the architecture and is flavoured by the attention restriction in the GOS, it becomes individual-based.

As a perspective, the proximate architecture for decision-making may be useful for some studies (e.g. behaviour in complex environments, personality variation and animal welfare) and overly complex for other purposes. So far, only fragments of the behavioural architecture of a generalized mesopelagic planktivore have been explored (Giske *et al.* 2013, 2014). While mesopelagic fish are a convenient group to study as they often form acoustic scattering layers allowing observations of short-term natural behaviour related to light, temperature, food and predators (Giske *et al.* 1990; Balino and Aksnes 1993; Goodson *et al.* 1995; Sørnes and Aksnes 2006; Kaartvedt *et al.* 2008; Staby and Aksnes 2011; Staby *et al.* 2011), we need studies on species where more of the basic biology is and will be known, such as three-spine sticklebacks (Bell and Foster 1994; Östlund-Nilsson *et al.* 2006; Wark *et al.* 2011) and zebrafish (Kalueff *et al.* 2012; Malafoglia *et al.* 2013; Cheng *et al.* 2014; Manuel *et al.* 2015), and on other species which can easily be studied in controlled experiments. A wide taxonomical and ecological range of study organisms is also important as the behavioural architecture will reflect macroevolution, life history and environmental factors (Sundström *et al.* 2005; Bell *et al.* 2010; Carretero Sanches *et al.* 2015). It will then also be natural to study how ‘slow’ learning experiences may be transformed to faster routinized responses. An interesting case on learning and survival circuits

is the observation that fish can recognize bodily responses related to danger in other individuals, which means they can read and utilize the 'expression of emotions in animals', in Darwin (1872)'s terms, and also learn to associate environmental cues with the cause of the GOS in other individuals (Mathis *et al.* 1996; Griffin 2004).

Any simple representation of nature, such as Fig. 1, is wrong for all that it omits (e.g. Warburton and Hughes 2011). Falsification would be easy, but a model has merits if it is useful. Breaking the model down to testable hypotheses amenable to experimental manipulation would make a stronger foundation for linking proximate with ultimate perspectives, models with experiments and basic science with application. Candidate cases for fruitful model/experiment interactions include which signals a GOS is most responsive to (e.g. Höjesjö *et al.* 2015), which GOS is activated when (e.g. Sundström *et al.* 2005), individual variation (e.g. Barreto and Volpato 2011), and how learning (e.g. Lehtiniemi 2005; Braithwaite *et al.* 2013) or changes in modulatory mechanisms (e.g. Giske and Aksnes 1992; Barber and Dingemanse 2010) upscale or downscale the importance of certain signals.

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