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OCEANS OF EMOTIONS: A NEW PERSPECTIVE ON ANIMAL BEHAVIOUR

Figure 1. Should I stay or should I go? A challenge for the curious cod! For this and many other challenges cod and most other animals rely on the emotion system. Photo: Jarl Giske

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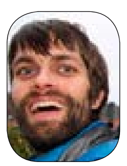

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Our own species has over the past few generations gradually expanded its influence until we now impact almost all ecosystems, and also most of the major populations on Earth. This impact has given us a strong responsibility to understand and monitor ecological dynamics. However, we do not have the capacity to be present everywhere anytime, and population modelling has therefore over the last decade increased in importance as a tool for understanding human impacts on the environment.

TROUBLE FOR THE RATIONAL AGENT

In most models of animal populations, behaviour is either ignored or poorly represented, due to a missing general methodology for modelling animal decision making and behaviour. Theories for animal behaviour have been developed for simplified scenarios, such as "what is optimal if behaviour depends on the age of the organism", or "if it depends on what the others do", or "if it depends on the physiology (e.g. fat reserves) of the animal". Also, it has helped a lot to assume that the environment does not change between generations, or that we know how it will change in the near future.

There is no way to calculate the best behaviour for organisms which shift between being constrained by physiology or by conspecifics, or are so simultaneously. And it is not getting easier if the organisms also live in environments where future conditions are hard to forecast. Indeed, studying populations of individuals with behaviour is a considerable problem that we have lacked unifying mathematical tools for.

Ever since biologists started using mathematical models, animal behaviour has been studied as a means of maximizing evolutionary fitness, through survival and offspring production. Hence, biologists have asked "How shall the bird behave during the winter day to avoid starving to death during the cold and long winter night?" or "How shall the fish move about so that it may return to the spawning areas alive and ready to spawn?" However, animals do not perform such calculations. How can organisms end up making evolutionarily sensible decisions without calculating the consequences (Figure 1)? And can their way of not doing these calculations guide us into more appropriate modelling methodologies? We think there is good empirical evidence to assume that animals use their emotion system for these calculations.

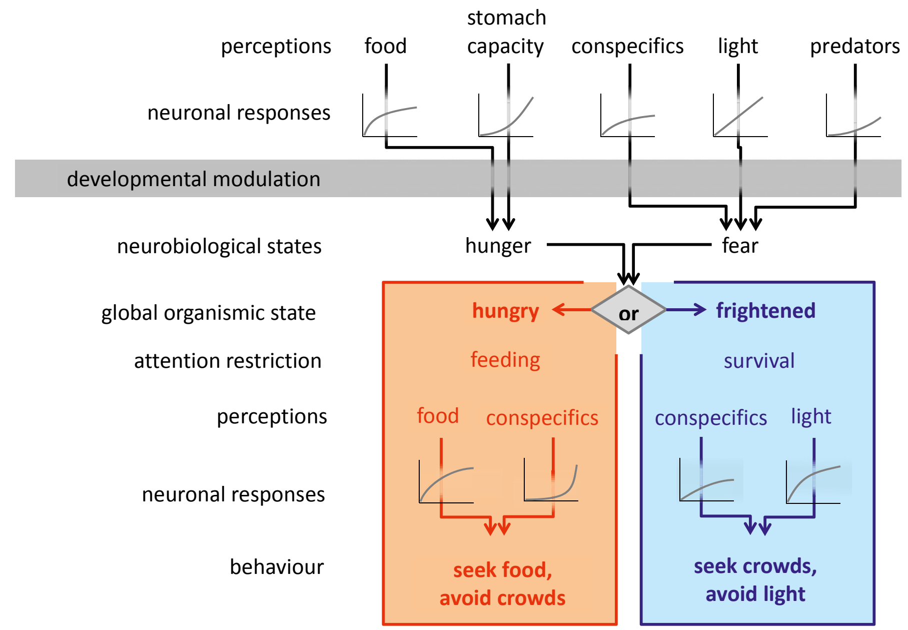

Figure 2. The emotion system's translation of sensory stimuli into behavioural responses in our model (Giske et al. 2013). Each type of sensory stimulus contributes to emotional appraisal through neuronal response, developmental modulation, and competition among hunger and fear. The strength of each neuronal response depends on two genes and can therefore evolve. Internal signals related to development are also genetic and may amplify the strength of inputs to hunger or fear. The emotional response starts with the stronger neurobiological state determining the global organismic state. The physiological response to this emotional appraisal includes attention restriction. In the processing of relevant behaviour, the emotion system thus re-evaluates a subset of its sensory information.

ENTER THE EMOTIONAL AGENT

While the emotion system is best studied and understood in humans, it is much older. The emotion system evolved from a system of "survival circuits" (LeDoux 2012), as old as life itself. Thus, while the word 'emotional' has a negative connotation in everyday language, the emotion system and the ancient system of survival circuits have a vital role as integrators of information and arbitrators of conflicting behavioural options.

In fish and their descendants – amphibians, reptiles, birds and mammals – the role of the emotion system is to integrate information obtained by the sensory system with the animal's motivation and its physiological state, and to use this to determine physiological and behavioural outcomes. For instance, if you see a bear during a hike in a forest, you will likely respond physiologically by increasing heart beat and by strongly focussing your attention, while your behavioural response may be to hide or flee, depending on the situation.

According to the survival circuit concept (LeDoux 2012), emotions are processes with a fitness-related survival function. The first half of the survival circuit is the emotional appraisal (Figure 2). It starts with sensory input, considers motivational impact related to age or developmental stage, and may potentially yield all-brain or even all-body activation into a global organismic state. The second half of the survival circuit is the emotional response, consisting of physiological responses and instrumental behaviour. Another way to put it is that the physiological activation enables the organism to focus its sensory attention, brain activity and potentially also bodily functions such as heart beat and muscle tension towards the present situation. The instrumental behaviour will try to satisfy the priorities of the global organismic state.

Fish are a convenient group for studying adaptive principles of the emotion system since they display both variation and consistency in behaviour but lack some of the higher cognitive functions that complicate the situation in other vertebrates and particularly in humans. We therefore address whether the emotion system can act as a general set of multipurpose rules in a fish model, where all rational calculations of future consequences are replaced by a simplified model of the emotion system in fish (Figure 2). This is, however, not to say that we have abandoned rationality for emotionality. Rather, we have moved the rational agent one level down: We do not assume that each individual performs rationality calculations, but we assume that the process of evolution gradually arrives at a well-balanced emotion system, which in the end serves the same purpose: individuals will tend to behave so that they maximize their chances of becoming parents and grand-parents.

ADAM AND EVE AND THE MEANING OF LIFE

As an illustration, contrast the positions of hedonic philosophy put forward by Socrates' student Aristippus with the Old Testament story of Adam and Eve. While the objective for mankind according to Genesis was to "multiply and fill the Earth", the Greek philosopher proposed that we should maximize pleasure in life, and never forsake an opportunity at hand for a possible later opportunity. In modern biological jargon, we would say that the Genesis objective is ultimate: it relates to the deepest or longest-term goals (fill the Earth). Aristippus' goal is proximate, as it relates to the here-and-now response to opportunity. In our model of the decisions of the fish, we have taken a proximate hedonic perspective: that each fish shall avoid hunger and danger in the short term. Each fish has no memory of past event or plan for the future, and makes its behaviour simply to diminish its presently most discomforting emotion of fear or hunger. However, as those individuals who are most successful in avoiding fear and hunger actually also end up as parents, it is their genes that will be passed on, and the population will be genetically changed from generation to generation until all genes code for ways to cope with hunger and fear. Hence, by following Aristippus' hedonic principle, our modelled fish also came to follow the ultimate commandment given to fish, according to Genesis: "multiply and stock the oceans".

EVOLUTION IN AN INDIVIDUAL-BASED MODEL

Technically, we let in our model a population of fish with fear and hunger live in a simulated ocean environment where some die young while others manage to survive and reproduce. For this we have developed an individual-based model of the population, with rich description of the environment. We then use a genetic algorithm to follow the population over a high number of generations, where offspring inherit genetic dispositions related to these emotions, such as how seeing more food increases hunger or how more light increases fear because they then become visible to their predators at a longer distance. They have two genes for each of the nine neuronal response functions in Figure 2, four for the developmental modulation and one gene which determines gender. Gradually, we observe the genes which were randomly created by us and given to the individuals in the first generation becoming replaced by such genes that give a fish appropriate emotions for its growth and survival, through blind mutations and natural selection in the computer. This modelling has taken place at the Parallab facilities in Bergen, with technical support from Uni Computing through a grant from Notur, and has so far given us 10 terabytes of data on simulated evolution in fish populations under a range of environmental conditions, with emphasis on adaptation of the genome, the emotion system, behaviour, and life history.

WHEN FISH LIVE OUT THEIR EMOTIONS

So what did we find? We found that even without long-term goals, the fish were able to live as if survival and reproduction were their goals. There are clear similarities between fish behaviour in our model and classical models of evolutionarily optimal decisions. We thus found that the emotion system can prioritize among competing demands in modelled organisms, as it does in natural organisms, and that the most important single factor for this to work is a mechanism of focussed attention. This is also just where modelling based on emotions differ from optimization models, since the latter generally will provide the 'agent' with all information available, while the emotion system filters out less relevant information.

We also found some interesting differences which we actually had not expected to see: we found personality types emerging in the evolving population. Maybe you already have concluded (from observing friends and colleagues?) that there is some connection between emotions and personalities, and that we had no reason to be surprised? However, consider the overly simplistic scheme of the emotion system in Figure 2, where the fish can have one of only two emotions and does not have many behavioural options available. Our surprise is that even in this very simplified scheme, populations tend to become divided into distinct personality types. For one thing, we see males taking more chances than females. This can be understood from the reproduction routine we have forced upon them, where each surviving female compares the size of the three first males she encounters in the final time step, and mates with the larger. But we also see sex-independent differences (Figure 3): Some individuals will, when hungry, ignore the presence of competitors, and search for the densest prey concentrations. Others will be uncomfortable when food competition is intense, and will prefer to feed in places with few other fish, even if prey density too is much lower there. Hence, we find that there is spatial structure in the population with regard to personality types.

One benefit of this approach is that a consideration of emotions in fish and other organisms takes us one step closer to how animals live and behave. Another is that focus on the mechanisms involved in behaviour facilitates dialogue between empiricists and theoreticians and across disciplines that study behaviour from various perspectives, such as genetics, physiology, psychology, neuroscience, and evolution. Finally, it opens for more realistic models of variations in behaviour among individuals in natural populations, both in the sea and on land, to the benefit of researchers in conservation biology and environmental studies.

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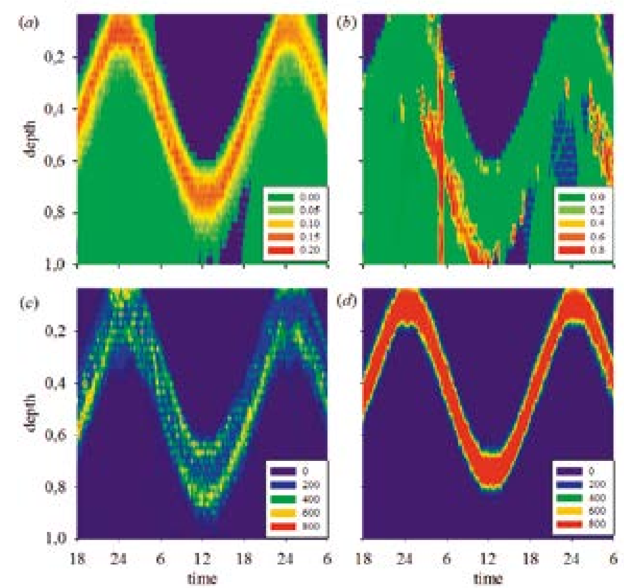

Figure 3 A) The fish population performs typical diel vertical migration (shown as the orange band) as also seen in classical optimization models, where individuals avoid the surface layer during daytime due to increased predation risk in illuminated waters. A few strayers, shown in green, have mutations or genes that make them behave otherwise. **B)** Most individuals are hungry (the scale shows proportion hungry, with green implying that all individuals are hungry while red areas are dominated by frightened individuals). Those who are afraid are generally found in the safest (deepest) parts of the vertically migrating population. Hence, being afraid is not only a question of the danger level, but also of the personality type. **C** and **D)** Individuals who try to avoid competitors when they are hungry (C) are found in the deep and shallow outskirts of the population, where there is both less food and low competition, while individuals with a personality type that ignores competitors when hungry (D) are located where food concentration is highest and competition stiffest.