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# From sensing to emergent adaptations: Modelling the proximate architecture for decision-making

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### ABSTRACT

During the past 50 years, evolutionary theory for animal behaviour has branched into different methodological frameworks focussing on age-, state-, density-, and frequency-dependent processes. These approaches have led to valuable insights in optimal responses, state dependent choices, and behavioural strategies in social contexts. We argue that time is ripe for an integration of these methodologies based on a rigorous implementation of proximate mechanisms. We describe such a modelling framework that is based on the architectural structures of sensing and information processing, physiological and neurological states, and behavioural control in animals. An individual-based model of this decision architecture is embedded in a genetic algorithm that finds evolutionary adaptations. This proximate architecture framework can be utilized for modelling behavioural challenges in complex environments, for example how animals make behavioural decisions based on multiple sources of information, or adapt to changing environments. The framework represents the evolution of the proximate mechanisms that underlie animal decision making, and it aligns with individual-based ecology by emphasizing the role of local information, perception, and individual behaviour.

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## 1. Introduction

Most theories for animal behaviour have traditionally assumed that individuals have accurate perception of the current environment, that they have full information on which to base their decisions, and that they make optimal choices independent of time constraints or the amount of computation required. This is in contrast to observations of animal behaviour where one would most likely conclude that animals are not smart but quite often do clever things. This apparent cleverness may stem from two sources at different time scales:

(1) Animals are flexible as they e.g. can respond fast and adequately in situations they have never experienced before. This suggests that behaviour is controlled by heuristics (Gigerenzer, 2004), where the proximate mechanism (the decision-making process) has an architecture that allows efficient information use and decision-making. This architecture enables minor changes

in sensory input (e.g. stronger signals of predator presence) to lead to very different behaviours (e.g. termination of feeding behaviour) or experience from one situation to be made useful in a novel context.

(2) Small evolutionary changes in this architecture may alter the behavioural phenotype quite substantially (e.g. van der Post and Semmann, 2011a), very similar to how small mutations in the regulation of developmental pathways can open up morphological diversity and innovations (e.g. Moczek et al., 2011). In the language of Tinbergen (1963), the proximate mechanism has an architecture that is particularly good at evolving as the ultimate drivers change.

As a result animal behaviour is controlled by proximate heuristic mechanisms that rest upon an innovative architecture. Still, the proximate mechanisms have largely been ignored in evolutionary and ecological models despite that they are (i) what evolve, (ii) what cause the emergence of behaviours one can observe in the wild and in the lab, and (iii) what can be studied in terms of neurology, physiology, biochemistry, and genetics. In this paper we describe the proximate architecture for decision-making, which represents biological processes from sensing via information processing and decision making through to the physiological and behavioural response. We argue that this framework is useful for understanding

Abbreviations: GA, genetic algorithm; GOS, global organismic state; IBM, individual-based model; NR, neuronal response.

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animal behaviour and that the proximate architecture can be incorporated mechanistically within an individual-based approach. With proper rooting in evolutionary adaptation, this may become an important tool for evolutionary and ecological modelling.

## 2. Behaviour in the individual-based paradigm

Evolutionary theory for animal behaviour has branched into different modelling frameworks focussing on age-, state-, density-, and frequency-dependent processes, with little integration between methodologies. The American statistician Alfred Lotka was the first to model evolutionary adaptation and behaviour, by turning the population growth equation of Euler (1760) into an equation for fitness (Lotka, 1907, 1925). In his interpretation of what we now call the Euler–Lotka equation, competing resource investments and activities of the organism are evaluated with a common currency: their contributions to the organism's expected rate of offspring production. The modelling paradigm is therefore based on the premise that organisms make optimal decisions. This tradition has developed further into life history theory (Fisher, 1930; Murdoch, 1966; Roff, 1992; Stearns, 1992; Williams, 1966), optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966; Charnov, 1976), game theory (Fretwell and Lucas, 1970; Maynard Smith and Price, 1973), and adaptive dynamics (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992).

While the Euler–Lotka equation, game theory and adaptive dynamics are population-based tools to understand individuals, optimal foraging theory and state-dependent life history theory (Mangel and Clark, 1986; McNamara and Houston, 1986) can be used and understood from a purely individual perspective. Although these methods are excellent tools in evolutionary ecology, none of them are all-purpose. Optimization techniques excel at finding the best possible solution to a problem without considering potential fitness valleys which may prevent the optimum itself from being reached. State-dependent life history theory is excellent for finding optimal policies when they depend on some (physiological) state of the organism, but at the expense of policies towards other individuals. The opposite is the case for the game theory tradition.

In the 1970s a different tradition, based on Individual Based Modelling (IBM; DeAngelis and Grimm, 2014; Huston et al., 1988) arose. This paradigm merged perspectives from artificial life (Langton, 1986; von Neumann, 1966) and artificial intelligence (Newell and Simon, 1956) with another major tradition in mathematical ecology, community ecology. The early papers of IBM focused on forest ecosystems (Botkin et al., 1972; Shugart and West, 1977, 1980) and fish populations (DeAngelis et al., 1980). The new tool was used to study population and ecosystem consequences of rare phenomena, such as the death of a canopy-forming tree or the survival of a larval fish through the earliest life stages. From this beginning, the individual based approach has given more flexibility in modelling ecological interactions, by allowing detailed representations of individuals living in complex ecological landscapes (Grimm and Railsback, 2005; Stillman et al., 2015). This is important because flexible and diverse behavioural responses generally observed in nature are not found in simplified models (Evans et al., 2012, 2013; Fawcett et al., 2012, 2014; McNamara and Houston, 2009). While ecology and evolution has been integrated in the artificial life tradition (e.g. Byrski et al., 2015; de Boer and Hogeweg, 2012; Paredis, 1995; Ray, 1994), the link to evolutionary dynamics in individual-based models has often been absent (Grimm, 1999).

In the following we will discuss some features of organisms that may be taken advantage of when modelling evolutionarily adaptive behaviours. These enable the integration of the ultimate perspective of optimization models with the proximate

mechanisms important in ecological interactions. There are many methods available for this, collectively termed multi-scale models by Hogeweg (2007). We will focus on the proximate architecture framework, which gives a representation of biological processes from sensing via information processing and decision making through to action for a wide range of animals. The framework can be utilized in ecological modelling, in particular for organisms that make decisions based on multiple sources of information, in complex, variable and even novel environments, where long-term fitness consequences of behavioural choices are unpredictable.

## 3. Behavioural control through the proximate architecture framework

In this section we describe some key elements in decision making and behavioural control in animals. As we move from the idealized environments typical for the Euler–Lotka models to moderately variable or complex environments, finding optimal responses to all possible situations would require highly advanced (Goldstein and Gigerenzer, 2011; McNamara and Houston, 2009) and energetically expensive brains (Nilsson, 2000). Natural organisms instead rely on simpler heuristics to handle large amounts and different types of information (Gigerenzer, 2004; LeDoux, 1998). These 'rules of thumb' have been selected to perform well in a variety of situations, including those never encountered before (Hutchinson and Gigerenzer, 2005).

Behavioural control in animals is organized as heuristics embedded within an architecture of other modules or functions of the organism. The architecture can be described as a series of weakly connected survival circuits (LeDoux, 2012) which link perceptions to behaviour. Also referred to as "the emotion system", it plays a central role in animal decision making (Cabanac, 1979; Leknes and Tracey, 2008; Mendl et al., 2009) through evaluation of perceptions and selection of the instrumental behavioural and physiological responses (de Waal, 2011; LeDoux, 2000, 2012; Panksepp, 2005). However, this proximate architecture is not limited to those concepts psychologists call emotions (Izard, 2010), as survival circuits exist for all drives that impact attention and behaviour of the organism (LeDoux, 2012). We emphasize that in using concepts often associated with human feelings, particularly the word "emotion" with reference to LeDoux's work, we do not imply any mental awareness of these internal processes in animals.

The architectural structure described above can be implemented in individual-based modelling (Fig. 1; Giske et al., 2013), and in the following we will sketch the process of decision making in this framework, leaving the more technical modelling aspects for Appendix. We use an example from fish behaviour to illustrate the concepts, but this specific formulation is only one possible way of outlining the proximate architecture (see e.g. Evers et al., 2014, 2015).

### 3.1. Biological mechanisms

Specific to the architectural approach is the level of detail of the representation of the chain of events from immediate perceptions to instrumental behaviour (Giske et al., 2013; LeDoux, 2012). First, all perceptions (including signals from within the body) are evaluated in the brain, where different competing needs are weighed against each other to determine the most important task. Next, the organism focuses on solving this task. LeDoux (2012) calls this chain from perception to behaviour a survival circuit, and animals can have several such survival circuits running in parallel. These may for instance be related to hunger, thirst, sleepiness, curiosity, and fear; thus we may say the survival circuits are bundled, as illustrated in Fig. 1. Each circuit has different modules; hunger

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