Integrating function and mechanism

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Behavioural ecology often makes the assumption that animals can respond flexibly by adopting the optimal behaviour for each circumstance. However, as ethologists have long known, behaviour is determined by mechanisms that are not optimal in every circumstance. As we discuss here, we believe that it is necessary to integrate these separate traditions by considering the evolution of mechanisms, an approach referred to as 'Evo-mecho'. This integration is timely because there is a growing awareness of the importance of environmental complexity in shaping behaviour; there are established and effective computational procedures for simulating evolution and there is rapidly increasing knowledge of the neuronal basis of decision-making. Although behavioural ecologists have built complex models of optimal behaviour in simple environments, we argue that they need to focus on simple mechanisms that perform well in complex environments.

Background

The traditional approach in behavioural ecology is to assume that optimal behavioural rules can evolve. Rules specify what to do in every possible circumstance, and can potentially specify a highly flexible plastic response. For example, Barta *et al.* [1] modelled the optimal annual routine of a migratory bird. In this context, the behaviour of a bird is allowed to depend on its energy reserves, feather quality, geographic location, and time of year. The rule for the bird specifies what to do for every combination of these state variables. Under an optimal rule, the bird responds optimally to every combination of variables [2]. To do so, its response to these variables must be flexible in that the action taken in one circumstance does not constrain what is done in other circumstances.

The assumption that behaviour depends on circumstances in a completely flexible way might not be realistic. Rules are implemented by psychological and physiological mechanisms, and the work of ethologists has shown that rules might be relatively inflexible, based on drives or schematic accounts of the real world. These rules are typically not optimal in all circumstances (Box 1). Tinbergen [3] pointed out that there are several ways in which behaviour can be explained, including mechanisms (causal explanations) and evolutionary consequences (functional explanations). Data show that purely functional accounts of behaviour will not be adequate [4], so it is necessary to integrate function and mechanism. Despite the fact that this has been advocated by many authors for decades,

much remains to be done and this integration requires a new impetus.

Behavioural ecology often concentrates on functional explanations. Mechanisms have not been ignored, but they tend to be seen as constraints on the options that an animal has [5]. For example, Houston and McNamara [6] found the optimal way to exploit patches given a constraint imposed by limitations on the ability to estimate how long has been spent in a patch. Related work by Kacelnik is discussed below. This work concentrates on the consequences of mechanisms rather than on their evolutionary origin. Neuroeconomics [7,8] aims to establish the neuronal basis of decision-making and, although it provides important insights, the fact that it relies on laboratory experiments restricts the environments that have been considered. Evolutionary psychology and cognitive ecology as envisaged by Dukas [9] include the analysis of optimal cognitive mechanisms. Work on this topic has investigated the performance of different types of rules, but often in relatively simple and specific environments (e.g. choice between feeding options when there is no risk of predation) [10]. However, real environments are richer and conclusions from simple environments might be misleading. For example, Seth [11] has shown that making a foraging environment richer by including competition can change what evolves. We advocate extending this sort of investigation. We believe that it is time for a systematic study of the evolution of mechanisms ('Evo-mecho') in environments that are sufficiently rich to capture the crucial features of the world in which mechanisms have evolved.

Evolution of rules

In the context of the evolution of mechanisms and the rules they implement, we identify three levels at which questions can be asked:

L1. Why are rules not completely flexible and why are they not optimal in all circumstances?

L2. For a given type of mechanism or rule, how is evolution expected to have tuned its details?

L3. Why do animals have particular organisational principles? For example, why base decisions on emotions such as fear? Why do animals exhibit associative learning and habituation?

We now elaborate on these three levels.

L1: why are rules not completely flexible?

In the model of a migratory bird [1], the circumstances of an individual bird are uniquely specified by a few simple state variables. If this model really was a description of the

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Box 1. Rethinking a classic: courtship in sticklebacks

During its breeding season, the male three-spined stickleback, *Gasterosteus aculeatus*, must establish and maintain a territory, build a nest to which his courtship behaviour attracts females, and drive away rival males that might attempt to destroy his nest, steal his eggs, or obtain fertilisations [65]. While carrying out all these activities, he also needs to avoid predators.

In an ideal world, a male could identify all stimuli correctly and adopt the appropriate optimal action. However, the behaviour that is observed does not conform to this ideal. Males are aggressive to females, might prefer to court a model rather than real females and display aggressively to model males [66]. (In other words, it is possible to construct 'supernormal' stimuli that are more effective than naturally occurring stimuli.) This behaviour is not surprising given that, in the real world, stimuli are ambiguous and the possibilities are too complex for the organism to store or compute the optimal action for every possible circumstance. A search for a more realistic alternative could start from the classic ethological view of courtship in sticklebacks as being based on an interaction between sex drive and aggression drive [66,67]. A possible starting assumption is that decisions are based on these motivational variables. Selection can then modify how these variables change and interact to produce a pattern of courtship that works well on average.

A model of the type described above has yet to be constructed, but it might predict the errors in behaviour that are observed. It might also result in motivational inertia, in that it might not be possible to switch immediately from aggression to courtship. Motivational inertia is seen in the courtship of the stickleback [68]. The extent to which it is adaptive (rather than a side-effect) has yet to be explored.

world, then the optimal rule could be implemented by looking up the optimal action to adopt in each state. However, the world is not as simple as this or any other model. The number of situations is too vast to expect the optimal decision for every situation to evolve [12]. Instead, it is likely that animals will evolve rules that perform well on average in their natural environment. These rules might be simple [13] and might not be exactly optimal in any situation (Box 1).

It might be possible to give a complete characterisation of some of the ways in which humans interact with the world. For example, Elle Woods says in the film 'Legally Blonde' 'The rules of hair care are simple and finite.' It is likely, however, that the complexities of social interaction cannot be effectively represented in this way. Baron-Cohen [14] argues that the inability of autistic individuals to deal with social life stems from their attempts to represent other individuals in terms of simple input–output relationships rather than by empathy (i.e. by using emotional responses). The importance of the complexity of social life in selecting for animals that understand each other is stressed by Humphrey [15].

Emotions provide obvious examples of general reactions to circumstances. For example, although there might be some specialised aspects of the response that are particular to the stimulus, fear is a generalised and stereotypical response to many stimuli. A possible reason for this lack of specificity is that the world is too complex: the types of dangerous situation are too diverse to have a rule specifying a separate response to each one [16]. Thus, the message is that the world is too complex for evolution to produce rules that behave optimally in every possible circumstance.

L2: for a given type of mechanism or rule, how is evolution expected to have tuned its parameters?

Given a mechanism or rule, optimisation and/or game-theory can sometimes be used to identify the optimal tuning of parameters. We start with two simple examples in which a Level-2 analysis has been carried out.

Hodgkin [17] argues that the properties of giant axons have been selected to enable the organism to react swiftly. Increasing the density of sodium channels has two effects. It increases velocity because of an increase in sodium conductance, but it decreases velocity because of an increase in membrane capacity. At low density, the first effect dominates, but at high densities the second effect dominates. Hodgkin showed that the density at which velocity is maximised is close to the observed density; see Ref [18] for further discussion. For discussion of selection on costs of information processing, see Ref [19].

Trimmer *et al.* [20] investigated how a mammal should respond to possible danger. It has been suggested that mammals have two decision-making systems in their brains. The subcortical pathway relayed through the thalamus operates quickly but is not accurate. The more recently evolved system, in the cortex, enables information to be gathered continually so that the accuracy of the decision increases over time. It is slower but more accurate than the thalamic system. Trimmer *et al.* found the best values of the system parameters given various patterns of information flow between the systems. Their analysis identified when one or other system should be more useful, and suggests why the older system has been retained.

Recent research on general features of mental organisation, such as attention [21] and sleep [22], provide further examples of Level-2 analyses. The work of McNamara and Buchanan [23] on the stress response illustrates a case in which a Level-2 analysis has been started but further work is needed. Taking the benefits and costs of a stress response as given, they analysed the optimal level of the stress response to cope with particular stressors. A stressor that is likely to be over quickly is predicted to elicit a strong stress response, whereas if the stressor is likely to be long-lasting, the animal cannot afford to maintain a strong stress response because of the damage that it will cause. Maladaptive effects of stress are thus likely to occur if an animal expects a stressor to be brief but experiences a prolonged stressor, which might be particularly likely in environments to which the animal is not adapted (e.g. captivity). Future work needs to link the stress response to real environments and, hence, account for the relationship between stress response and ecology. More fundamentally, are there good functional reasons for the deleterious physiological effects of the stress response?

Associative learning is concerned with the way in which animals associate stimuli with outcomes, and here there are many open questions. Data from laboratory experiments can often be described by the Rescorla–Wagner equation [24] (Box 2). Bitterman [25] notes that this equation accounts for the behaviour of a range of animal species, but the parameters of the equation differ across species. Why should this be? Any attempt to answer will need to address performance under the range of conditions in which a species might have to learn [26]. This means

Box 2. Classes of rules: Rescorla–Wagner and hyperbolic discounting

We illustrate the concept of a class of rule using two examples: the Rescorla–Wagner equation for associative learning and the hyperbolic discounting equation.

A class of rules for associative learning

The Rescorla–Wagner equation [24] for associative learning is concerned with how the strength of association for a particular alternative depends on the rewards previously obtained from that alternative. A simple version of the equation for the change in strength $\Delta X(t)$ as a result of reward has the following form (Equation I):

$$\Delta X(t) = \alpha[\lambda - X(t)] \qquad \text{(Eqn I)}$$

where λ depends on the reward magnitude and α is a learning parameter.

This can be re-written to express the new value of X as Equation II:

$$X(t+1) = \Delta X(t) + X(t) = \alpha\lambda + (1-\alpha)X(t). \qquad \text{(Eqn II)}$$

Thus, the updating of X is performed by a linear operator that gives weight $1-\alpha$ to the previous strength and weight α to the new reward. Rules of this class differ in terms of α. Because α determines the relative weight given to current as opposed to previous experience, the rate of environmental change should influence the value of α that evolves [69,70].

A complete account of learning has to specify the strength of association and how these strengths determine behaviour. A Level-2 question is which value of α will evolve, whereas a Level-3 question is why is learning described by the Rescorla–Wagner equation?

A class of rules for discounting the future

Mazur [51,52] has shown that the choice between options that differ in terms of amount of food A and delay until food is obtained D can be explained by assuming that the value of an option is given by Equation III:

$$V = \frac{A}{1 + kD}, \qquad \text{(Eqn III)}$$

where the constant k is the discount parameter. This is known as 'hyperbolic discounting'. A Level-2 question is 'which value of k will evolve?', whereas a Level-3 question is 'why is discounting hyperbolic?'

that it is necessary to consider a complex model environment that incorporates this range. McNamara [27] makes the same point in the context of risk-sensitive foraging. He argues that the discrepancy between existing theory and the data arises because the theory is based on an environment that is too simple compared with the real world.

Our examples show that questions at Levels 1 and 2 can be relatively straightforward. In contrast, questions at Level 3 tend to be more challenging.

L3: why do animals have particular organisational principles?

We outline several questions that are fundamental to animal behaviour and psychology. Although the questions are easy to pose, in no case do we have a compelling answer to why the feature exists. The best that we can say is that, in some cases, a possible intuitive justification can be given.

Mental accounting (i.e. the process by which humans keep track of financial gains and losses) does not always follow the principles that would be expected on the basis of rational decision-making [28]. For example, money in one mental account is not always a perfect substitute for money in a different mental account. A Level-2 analysis would take the accounting procedure as given and then ask how to exploit it. For example, a welfare economist might consider how to design a saving scheme that encouraged people to save in prudent ways, whereas an advertiser might be interested in how to design an advertising campaign that results in a substantial profit. The fundamental (Level 3) question is why humans have these accounting principles.

Kahneman and Tversky [29] note that humans perceive outcomes as gains or losses with respect to a reference point rather than as the resulting wealth. This assumption describes the data but leaves the reason for such a perception unexplained. The simplest fitness argument would be based solely on the final wealth and not on the difference between the final wealth and a reference level of wealth. To answer the Level-3 question, it is necessary to explain why this obvious approach is inadequate and demonstrate why a reference-based system might be advantageous.

In psychophysics, Weber's Law is the observation that the detectable increase in the magnitude of a stimulus divided by the initial magnitude of the stimulus is constant. That is, it is easier to detect a given change in a small stimulus magnitude than in a large one. Kacelnik and colleagues [30,31] have shown how this law (or generalisations of it) can explain how animals choose between stochastic rewards that differ in terms of expected magnitude and delay (i.e. the implications of the law have been determined). But why should the law hold? To what extent is it a psychophysical constraint as opposed to an adaptive outcome?

A general issue that has been debated in the literature on human and non-human animals is whether cognition is modular (i.e. is based on 'multiple distinct processes rather than a single undifferentiated one') [32], see also Ref [33]. Livnat and Pippenger [34] argue that not only should we expect distinct modules or drives, but these drives should also have competing goals. Some aspects of the modular view of the brain are denied by Bitterman [25] and Macphail and Bolhuis [35], who argue that the laws of learning are general. Although it might not be straightforward to establish what is meant by modules, we believe that further theoretical work on the evolution of modular brains is warranted.

The mental life of an animal can be analysed in terms of the way in which emotions are organised. One view is that there is a basic set of discrete emotions (e.g. fear, anger, sadness, happiness) [36]. By contrast, it has been argued that mental state of an animal has two core dimensions, valence (pleasure through to displeasure) and arousal (high through to low levels of physiological activation) and that each emotion is based on a specific combination of these variables [37,38]. Can anything be said about which alternative is likely to evolve? Moreover, why are emotions experienced in the way that they are? For example, the suggestion that the withdrawal behaviour that results from depression is useful in enabling a person to avoid unprofitable interactions or to reassess options does not explain why the depressed individual feels terrible.

If we accept the way in which hormones act as being fixed, we can ask a Level-2 question: what is the best way to

release hormones? For example, given a specification of the action of testosterone, we could investigate how natural selection should tune the way in which testosterone increases when a male sees a rival male and decreases once an interaction is over. The tuning would depend on social organisation, and could be compared with the observed trends [39,40].

Hormones typically have more than one effect [41,42]. Does this impose a constraint on the flexibility of the behaviour of an animal? Lessells [42] argues that there is little evidence in favour of hormonal constraints. She points out that the multiple effects of a hormone often make adaptive sense. The fact that some effects of a hormone can be removed shows that effects are not fixed. For example, testosterone typically increases aggression and courtship in male birds, while decreasing parental care. In some species of birds, male help with raising the young is important but, in these species, testosterone does not inhibit male care [43]. Further work is needed to establish if evolution can typically uncouple different consequences of a hormone.

The actions of hormones raise some interesting general issues. It is clear why hormones should produce physiological effects and why sensory inputs and mental states influence the release of hormones. However, it is less clear why hormones should then feed back to influence mood.

Although physiologists have often adopted an evolutionary approach, we believe that many aspects of physiology can be understood only by considering a richer environment than has been usual. For example, the metabolism of an animal must cope with fairly predictable periods of hard work (e.g. raising young), but also the unpredictable and stressful demands imposed by predators and the weather [44]. To predict the sort of metabolism that an animal should have, it is necessary to know the frequency and severity of these events. This can lead not only to Level-2 questions: (e.g. what value of basal metabolic rate do we expect?), but also to Level-3 questions about how physiology is organised. As a particular example, many species change their physiology according to circumstance [45]. We can understand the evolution of such flexibility only if we know the sort of environment that the animal encounters. Symmorphosis assumes that the performance of each component of the physiology of an organism is tuned to the demands imposed by other components [46]. In a realistic environment, this cannot always hold because demands fluctuate. Variable demands, as considered by Alexander [47], are needed to generate realistic predictions.

Even if interest is focussed on behaviour, it might be necessary to give an integrated account that includes physiology. Behaviour sets physiological demands; physiology determines the effectiveness of behaviour.

The way ahead

Level-3 questions are concerned with why animals have particular organisational principles. We believe that these questions are the most important but also the most neglected. We have identified a major challenge for accounts of behaviour: the integration of mechanism and evolution, where mechanism might be psychological, physiological or a combination of both. We have argued that, because they

face complex environments, animals have mechanisms that are not exactly optimal in any particular circumstance. An understanding of the evolution of mechanisms requires a fundamental change in the sort of models that are analysed. Instead of building complex models of optimal behaviour in simple environments, attention should be given to understanding the sorts of simple mechanisms that will evolve in complex environments. To do this, two questions must be addressed. First, what classes of rules should be considered? By rules of a particular class, we mean rules that have the same form but differ in their parameters (Box 2). Second, what range of environments should be considered?

Answering these questions might not be easy; it is the central difficulty in carrying out a Level-3 analysis. If these questions can be answered, the action of natural selection can be determined by adopting an evolutionary approach. Possible evolutionary techniques include genetic algorithms [11,48] neural networks [49] and genetic programming [50]. Each approach has advantages and disadvantages. Neural networks represent the relationship between sensory inputs and behavioural decisions. They have the advantage of biological plausibility, but interpreting the behaviour evolved by a neural network and relating it back to existing theory is not always easy. Genetic algorithms involve the explicit coding of a rule, but the way in which the rule is coded can influence the results. Genetic programming results in rules that can be interpreted, but they might contain redundant components.

We illustrate the evo-mecho approach in the context of self-control. There is widespread interest in the effects of delays before rewards are obtained on the choices that animals make [8,51–57]. In this context, animals are often said to be impulsive in that they prefer immediate over delayed rewards, even if waiting results in a higher rate of gain.

There are several approaches to explaining this behaviour. If future rewards are devalued because foraging might be interrupted, exponential discounting would be expected [58], but this form of discounting is not supported by the data [51,57]. Mazur [51] says that choices between two options are well described by hyperbolic discounting (Box 2). Kacelnik [57] argues that the appearance of hyperbolic discounting is a consequence of maximising net rate of energetic gain, where the calculation of rate does not include the delay between the choice times (the inter-trial interval). Kacelnik explains this in terms of the way that animals learn the consequences of various actions; times that are common to both choices are not associated with either choice. By contrast, Stephens [53] argues that comparing options by using the ratio of their rates will be more accurate if the inter-trial interval is ignored.

A possible Level-2 analysis would accept hyperbolic discounting and then find the best value of k for given circumstances. A full investigation of the evolution of discounting would involve not only optimising the parameters for any particular rule (Level 2), but also establishing which class of rule is best (Level 3). A Level-3 analysis would have to investigate the general effect of amounts of food and associated delays on reproductive success, *cf.* Ref. [59]. It would be necessary to

consider a range of environments and circumstances. For example, models based on energy delivery could be used to explore the behaviour of parents feeding young [60]. Environments could differ in terms of the distribution of food items (e.g. whether items are encountered simultaneously or sequentially). Models based on long-term survival could investigate the performance of rules in environments that differ in terms of the distribution of food and the risks of predation [61] and interruptions as a result of bad weather [62] or encounters with predators [63]. If rules are flexible, then different sorts of rule (or parameters for a given type of rule) might evolve in different circumstances. If rules are not flexible, then it is necessary to evolve rules that perform well on average over all circumstances. As Ydenberg *et al.* [64] say

'After a long absence from the scene, 'rules of thumb,' based on a deeper appreciation of mechanisms, are poised for a re-emergence.'

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