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Editorial

The Evolution of Mechanisms Underlying Behaviour

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1 Tinbergen's Vision

More than any other single work, Niko Tinbergen's landmark paper "On aims and methods of ethology" (Tinbergen, 1963) shaped the scientific study of animal behaviour and continues to be a guiding influence on the field (Manning, 2009; Barrett et al., 2013; Bateson and Laland, 2013; Dawkins, 2014; Strassmann, 2014; Taborsky, 2014). Building on the work of Huxley (1942), Tinbergen identified four broad, complementary questions we can ask about a behaviour, which in modern terms can be phrased as follows: How does the behaviour arise from underlying psychological, physiological and molecular processes (*mechanism*)? How does the behaviour develop within the organism's lifetime (*ontogeny*)? How does the behaviour affect the organism's fitness (*adaptive significance*)? How has the behaviour changed over evolutionary history (*phylogeny*)? Each of these questions forms a major area of contemporary research on animal behaviour (Barnard, 2004).

As well as differentiating these key research questions, Tinbergen (1963, p. 411) insisted that 'a comprehensive, coherent science of Ethology has to give equal attention to each of them *and to their integration*' (our emphasis). Yet, by and large, his four questions have been studied in parallel, neglecting the close links between them. For example, research on the adaptive significance of behaviour, the primary focus of behavioural ecology (Taborsky, 2014), has been largely separate from genomic and transcriptomic studies on the molecular mechanisms underpinning behaviour (e.g. Sokolowski, 2001), although there are signs that this is beginning to change (O'Connell and Hofmann, 2011; Ledón-Rettig et al., 2013; Zuk and Balenger, 2014). While the four questions refer to different levels of explanation and should not be confused with one another (Bolhuis, 2009; Scott-Phillips et al., 2011; Dickins and Barton, 2013; Hogan, in press), it can be misleading to study them in isolation. Recognition is growing that the four aspects of behaviour may interact and influence one another, requiring formal integration of 'proximate' (mechanistic and ontogenetic) and 'ultimate' (adaptive and phylogenetic) perspectives (McNamara and Houston, 2009; MacDougall-Shackleton, 2011; Laland et al., 2013; Hofmann et al., 2014; Monaghan, 2014; Lefebvre, in press). As Strassmann (2014) has argued, some of the most insightful studies of animal behaviour have fused two or more of Tinbergen's questions.

2 Evo-mecho

The survival value of behaviour was a subject close to Tinbergen's heart and the emergence of behavioural ecology as a vibrant research field was one of the clearest impacts of his legacy (Taborsky, 2014). Yet the success of the adaptationist perspective in explaining behaviour led to other levels of explanation being neglected (Dawkins, 1989). In focusing on optimal behavioural phenotypes, standard approaches in behavioural ecology make the implicit assumption that behaviour is unconstrained by the psychological, physiological and molecular mechanisms that produce it (the 'phenotypic gambit' [Grafen, 1984] and the 'behavioural gambit' [Fawcett et al., 2013]). This ignores the fact that natural selection can only modify behaviour by modifying the underlying mechanisms. To address this problem, McNamara and Houston (2009) advocated the integrated study of adaptive significance ('function') and mechanism. This approach, dubbed 'evo-mecho' (McNamara and Houston, 2009), investigates the evolutionary properties of the mechanisms themselves, rather than their behavioural outcomes.

It is important to recognise that the evo-mecho approach means more than conducting mechanistic studies of behaviour alongside studies of adaptive significance. Opening up the 'black box' of underlying mechanisms and examining the contents will not, in general, lead us to a deeper understanding of adaptation (Zuk and Balenger, 2014). Rather, evo-mecho demands that we explicitly integrate two of Tinbergen's questions, by considering how evolution has shaped the psychological, physiological and molecular mechanisms that produce behaviour. This is an ambitious goal, but there are signs that researchers are embracing the challenge. In this special issue of *Current Zoology* we document some of the recent developments, showcasing an emerging line of research that directly addresses the evolution of mechanisms underlying behaviour.

What precisely is meant by a 'mechanism'? Here we adopt a broad, inclusive view, reflected in the contributed articles, which address the evolution of a dazzling array of phenomena all linked to behaviour: hormones, genetic architecture, sensory organs, cognitive maps, cross-inhibitory drives, foraging strategies, search rules, spatial memory, associative learning, brain structure, mental representations and neural morphology. Thus the term 'mechanism' captures all of the internal processes that influence the expression of a particular behaviour—as Tinbergen (1963, p. 416) put it, 'physiology of behaviour … all the way down to molecular biology'. In this we also include psychological constructs such as emotional states, learning rules and cognitive biases, which are linked to patterns of behaviour and—although Tinbergen might not have approved (Manning, 2009)—can be studied from an adaptive perspective (e.g. Giske et al., 2013; Trimmer et al., 2013; Dridi and Lehmann, 2014; Fawcett et al., 2014).

3 Key Questions

The collection of articles here arose from a two-day meeting on 'The Evolution of Behavioural Mechanisms' (www.tinyurl.com/winterasab2013), which we (TWF, ADH and Pete C. Trimmer) organised in conjunction with the Association for the Study of Animal Behaviour (ASAB) on the 50th anniversary of Tinbergen's (1963) classic paper outlining the four questions. The meeting attracted a diverse mix of behavioural biologists, psychologists, neuroscientists and computer scientists all interested in the fusion of adaptive and mechanistic perspectives on behaviour. Empirical and theoretical approaches were both well represented and we have deliberately recreated that balance here, alongside review articles that develop and critically evaluate fundamental concepts of evo-mecho. Among the key issues discussed are: What are the limits to adaptive behaviour? How do the costs of neural tissue constrain behaviour? How do simple mechanisms allow behavioural flexibility? How does cognition interact with the environment? What are the evolutionary origins of advanced cognitive processes? In addressing these questions our special issue spans the full gamut of mechanisms, from gene sequences all the way to consciousness and creativity.

3.1 What are the limits to adaptive behaviour?

Behaviour may be constrained from reaching phenotypic optima by the limits and costs imposed by underlying mechanisms (DeWitt et al., 1998), or even by the details of the underlying genetic architecture itself (Moran, 1964). Versace (2015, THIS ISSUE) discusses how genomic resequencing combined with experimental evolution is revealing the genetic limits of behavioural adaptation, directly challenging the phenotypic gambit (Grafen, 1984). As a case study, she outlines an application of this approach to investigate the evolutionary dynamics of associative learning in *Drosophila*. Another constraint on optimal behaviour is the cost of switching between two actions that cannot be performed simultaneously, which is investigated in a mathematical model by Marshall et al. (2015, THIS ISSUE). Reviving the old ethological concept of 'drives' (Hinde, 1956), Marshall et al. show that cross-inhibition between competing motivations can help to reduce costly dithering and improve the efficiency of behaviour. The broader importance of trade-offs in constraining behavioural evolution is explored in more depth by Bastiaans and Swanger (2015, THIS ISSUE). They present a cross-classification of the major types of life-history trade-offs (allocation, acquisition and specialist–generalist, based on Angiletta et al., 2003) and three types of mechanism that may generate variation between individuals in the resolution of those trade-offs: genetic polymorphism, developmental (irreversible) plasticity and short-term (reversible) plasticity. Bastiaans and Swanger then apply this framework to a particular case study, the role of juvenile hormone in trade-offs in insect development, life history and behaviour.

3.2 How do the costs of neural tissue constrain behaviour?

Greater complexity or flexibility in behaviour may require a higher investment in the brain and other neural tissue that supports it; natural selection will favour a level of investment that optimally balances the benefits against the unavoidable energetic costs (Atwell and Laughlin, 2001). Three articles in our special issue consider the extent to which behavioural adaptations are related to differences in the brain, in terms of its overall size, gross structure and neural morphology. Corral-López et al. (2015, THIS ISSUE) use artificially selected lines of guppies *Poecilia reticulata* to investigate whether evolutionary changes in brain size affect male sexual behaviour. Their findings raise questions about the extent to which male courtship in this species is a cognitively demanding behaviour. Soares et al. (2015, THIS ISSUE) present a preliminary analysis of the co-variation between brain measurements and cooperative behaviour across four labrid fish species, finding evidence for differences in the size of specific brain regions but not in overall size. They argue that the cognitive demands associated with cooperative cleaning interactions have resulted in selective investment in certain brain regions at the expense of others. Finally, Robinson et al. (2015, THIS ISSUE) perform a phylogenetically controlled analysis using six lizard species to show that the relative use of visual versus chemical displays has evolved in concert with the density and size of neurons in brain areas associated with those communication modalities.

3.3 How do simple mechanisms allow behavioural flexibility?

Selection for efficient performance has resulted in mechanisms that can achieve a remarkable degree of behavioural flexibility despite their apparent simplicity. Pfuhl et al. (2015, THIS ISSUE) explain how the simple auditory system of moths—comprising no more than four sensory cells—underpins flexible and context-dependent behavioural adaptations to escape from echolocating bats. They also discuss the higher-level processing mechanisms in the brain that enable the moths to integrate multimodal cues. Higginson et al. (2015, THIS ISSUE) model the trade-off between the costs and benefits of flexibility in foraging behaviour, comparing a genetically evolved rule (subject to metabolic costs) against the optimal strategy found by dynamic programming. Their analysis reveals that, although the costly evolved rule is less accurate than the optimal strategy, the ability to generalise behaviour across similar sets of conditions gives it a key advantage in complex environments, where the situations encountered by individuals may have never been experienced by their ancestors. Continuing the theme of behavioural flexibility, Hesselberg (2015, THIS ISSUE) reviews the web-building behaviour of orb-web spiders, which, despite the apparent constraint of a small brain, can precisely adjust the geometry of their web to fit the local spatial surroundings. Although the web itself is complex and highly structured, it may be a product of relatively simple rules for responding to information from the previously laid threads.

3.4 How does cognition interact with the environment?

The next set of articles all highlight the point that mechanisms can only be understood in terms of how they interact with and exploit statistical features of the environment (see also Fawcett et al., 2014). Sulikowski and Burke (2015, THIS ISSUE) present a critique of the problem-solving tasks commonly used to investigate cognitive mechanisms in the laboratory, arguing that they often lack appropriate ecological context and fail to replicate the informational properties of the natural environments in which those mechanisms evolved. They advocate a more ecologically informed approach that considers how the informational properties of a task interact with the functional goals of the animal to produce observed behaviour. Arbilly (2015, THIS ISSUE) discusses the use of individual-based simulation models to investigate the evolution of learning and decision rules. Because details of the learning process are specified explicitly in these models, the costs of learning and the dynamics of information flow emerge from an individual's interactions with its (physical or social) environment rather than being imposed externally, which can alter predictions in interesting ways. Taking one such simulation approach, Kolodny et al. (2015, THIS ISSUE) show how 'creative' behaviour—novel sequences of actions that are adaptive on average—can arise from an internally represented network that learns about statistical regularities in the environment.

3.5 What are the evolutionary origins of advanced cognitive processes?

The special issue concludes with two articles exploring the evolution of mental representations. Hills and Butterfill (2015, THIS ISSUE) present evidence for a homology between foraging for resources in the external environment and foraging for items stored internally in memory, both of which may involve area-restricted search. They propose that certain forms of internal search allow individuals to predict the outcome of future actions, but that this relies on the ability to distinguish real from imagined outcomes, which is arguably a precursor of self-awareness. Ramírez and Marshall (2015, THIS ISSUE) formally evaluate Trivers's (2011) self-deception hypothesis, which posits that individuals can more effectively deceive others by first deceiving themselves. Their model explores the conditions under which it is advantageous for individuals to form a biased perception of their own fighting ability, under the assumption that honestly revealing this self-perceived ability is less costly than signalling dishonestly.

The diverse contributions to this special issue of *Current Zoology* present a snapshot of cutting-edge developments in evo-mecho research, which we hope other researchers will be inspired to build on and push the field in new directions. All of the articles raise more questions than they answer, which is a strong sign of a fruitful research endeavour. Together, they offer a compelling argument for the insights to be gained from an integrated approach that synthesises studies of the adaptive significance of behaviour and its mechanistic underpinnings.

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