Adaptive Behavior 2000, 8(1), 73-77

The Design of Animal Communication

EZEQUIEL A. DI PAOLO
University of Sussex, Brighton, BN1 9QH, UK

The Design of Animal Communication by Marc D. Hauser and Mark Konishi (eds). MIT Press, 1999, (xi + 701), $65.00 - £ 40.50 ISBN 0-262-08277-2.

Most students of animal behaviour would be willing to concede that much is known about a certain behaviour when one is able to provide satisfactory answers to Tinbergen's four questions in ethology, namely: what are the mechanisms underlying the production of the behaviour; what is its adaptive significance; how does the behaviour develop; and what is the evolutionary history that leads up to it. Without necessarily accepting all the distinctions implied in these questions, or their comprehensiveness, the twenty four chapters that comprise this hefty volume on animal communication can be said to be organised around a Tinbergenian ideal. The four questions almost invariably resonate within each chapter and between them. As such it is an ideal source of up-to-date information for researchers interested in modelling different aspects of adaptive behaviour.

The book is the outcome of a symposium held in 1997 to honour the scientific trajectory of Peter Marler. Many of the contributors to this volume have been his students or collaborators, and they all recognize his influence with gratitude. It is no wonder then that nine of the twenty four chapters are somehow concerned with the class *Aves* and that the prevalent modality of communication discussed is acoustic (18 chapters). Also, certain themes which can be directly linked to pioneering work by Marler and colleagues recur frequently, e.g., genetic dispositions in learning, sensitive periods, categorical perception, etc.

The three divisions of the book are: "Mechanisms of Communication", "Ontogeny of Communication", and "Evolution of Communication". There is a healthy amount of thematic overlap in some of the chapters although no one chapter succeeds in presenting a fully comparative approach to the four ethological questions. Almost all the articles are of the review type, bringing to the reader valuable and often recent experimental information and occasional theoretical discussions and speculations. There is, however, a conspicuous lack of modelling in this book (with one notable exception in the last part), even in cases that seem to be crying out for it. Researchers engaged in the construction of mathematical and simulation models with application to animal behaviour will find a clear exposition of some of the most pressing problems in these areas to which different modelling techniques may be suitable. Likewise, some of the chapters will provide a source of inspiration for researchers involved in transferring knowledge from biology into engineering contexts.

The first part is, generally speaking, the most solid. In it we find pieces such as Michelsen's on the dance language of honeybees, which describes with clarity how much there is still to know about the way the dance is perceived by the recruits. Hypotheses include vibrations in the comb wall produced by the wagging run of the recruiter, touch, and air currents produced by wing vibrations. Evidence for and against the different modes and the kind of information that may be transmitted through them is reviewed in detail. The chapter includes fascinating experiments using a robotic dancing bee which is able to imitate various dancing modes, thus permitting the subsequent study of recruit behaviour. This is one of the very few successful cases of using robots to test the response of real animals. With similar goals, is Kanwal's chapter on the neural processing of calls in echolocating bats. In contrast, the chapter by Kelley and Tobias is focused more on mechanisms of signal production rather than perception. South African clawed frogs produce sexually

dimorphic signals by which females and males are attracted to each other. The character and function of the different signals can sometimes reveal interesting pair interactions such as the performance of duets. Much of the sexual differences in signalling behaviour is attributable to structural differences in the larynx which occur during development and less to specific differences in neural dynamics.

Two key chapters deal with song mechanisms in songbirds. Suthers reviews the motor basis of vocal performance showing how much versatility is derived from a structural component common to most songbirds. The bipartite structure of the sound organ, the syrinx, allows a series of strategies showing left-right specialization in vocal registers and frequency modulation. The strategies range from independent bilateral phonation (the simultaneous production of two different voices) to left-right alternation and unilateral specialization. In this way the same basic structure can give rise to large acoustic diversity in oscine birdsong. Nottebohm contributes what is perhaps the most comprehensive review on the anatomy and timing of vocal learning in songbirds ever written. It offers an account of at least 30 years of research on neural and developmental mechanisms of song learning, maintenance, production, and perception including recent exciting findings regarding the influence of song perception and production on lower level phenomena such as gene expression and on neurotrophic factors that regulate neural survival. Along with the richness of information contained in this review, the chapter is of special interest to modellers because it points clearly to the hot unanswered questions in the field.

Two other chapters focus more specifically on neuroendocrine mechanisms in songbirds. Ball reviews the mechanisms of seasonal changes in vocal behaviour in songbirds, particularly in temperate areas, while Wingfield et al. review the ecological bases of testosterone regulation and its influence on aggression and communication.

The remaining chapters in this first part overlap a little and are concerned with mechanisms for recognizing emotions and postures in primates. Perrett presents evidence from single-neuron recordings in anesthetized macaque monkeys to whom static pictures and films are presented of people in different postures. Little is said about how these neural correlations are to be related to the communication behaviour of the unanesthetized animal or how their representational role is justified. This chapter is only tenuously related to communication. Adolphs does a better job in this sense; he is concerned with the perception of emotions in humans and reviews evidence based on brain lesions.

The second part of the book opens with a chapter by Peter Marler on the meanings of the terms 'innate' or 'learned' in the context of birdsong development. Rather than presenting a purely theoretical analysis of the poverty of the nature-nurture dichotomy, he engages in the much more direct approach of very clearly discussing (now classic) experiments in song learning in different species of sparrows. Roughly speaking, song learning proceeds in two different phases: one of 'model acquisition' in which the bird is exposed to mature songs but does not sing, and a later sensorimotor phase in which the song is practised and after which the bird is capable of reproducing the song. Birds raised in isolation, i.e., with no model to copy, develop atypical songs which nevertheless conserve some of their species-typical characteristics. This suggests that innate dispositions are at play and constrain what a bird can learn. This suggestion is backed up by evidence from the more stringent case in which auditory feedback is removed during development by deafening the birds. The resulting songs are almost structureless but still some differences occur between the species. Marler concludes that to say that birds learn their songs in the sense that these are 'picked up' in their entirety from their environment is as incorrect as saying that they do not need experience to develop them. The dichotomous reading of the terms 'innate' and 'learned' "is not only logically flawed, but actually hinders progress in understanding the principles underlying behavioral development", (p. 312). For additional, more subtle evidence one need only turn back a few pages to Nottebohm's chapter and re-read how song perception and production can influence gene expression and regulate neural survival.

Related ideas appear in Mundinger's chapter on the genetics of canary song learning. Experiments with two different strains of canaries show differences in the ease with which they are able to learn the wild-type song. Backcross breeding experiments allow something to be said about the genetics of the learning system: for instance, that it is likely to be a case of multifactor inheritance (possibly multi-chromosome)

and that it is sex-linked. Mundinger repeats a point made by Marler about using these studies in a differential way (as in population genetics) to account for phenotypic variations in learning, and how they correlate with genetic variations. This is a correct usage of genetic studies, but one must take into consideration that the outcome of such studies is always a correlation and not a causal link as Mundinger often seems to imply. In this respect it is important to emphasize that causal links cannot be explained exclusively in differential terms but need, in contrast, an account of the developmental process that makes two systems *similar* rather than *different*. Why do songs resemble one another for a given species?

The question of the *ecological significance* of behaviour can be said to lie at the intersection of Tinbergen's developmental, adaptive and evolutionary questions, but also to map a territory not often explored by the latter. From this angle, Kroodsma reviews the patterns of geographical variation in the chestnut-sided warbler. Intersexual courtship songs show low variation and intrasexual aggressive songs show high variation. He concludes that this is the outcome of two different developmental strategies: learn an average song from everybody in the first case, and learn a local song from your territorial neighbours in the second. This apparently confers the advantages of being able to match the repertoire of your specific neighbours while being also able to attract dispersing females (proposed advantages that would benefit from some quantification). Kroodsma fails to explore alternative hypotheses. For instance, there could well be stronger developmental dispositions, such as those described by Marler, in the case of courtship songs that would account for their low geographic variation, while the variability in aggressive songs could perhaps be explained by an adequate strategy of territorial preferences where local songs could play a role in a bird settling in a territory. These are equally speculative hypotheses but a discussion of these or other hypotheses would have enriched the review, particularly since it deals so well with the interactions of many other ecological factors such as density-dependence. From a theoretical angle, the exploration of these alternatives could well be approached by the use of individual-based evolutionary modelling.

Doupe and Solis review the selective neural responses in different brain nuclei in songbirds. They attempt to explain the period of song 'memorization' and the sensorimotor period by identifying what centres could be playing the role of 'memory templates' which would be formed in the first period and used to perform some sort of 'matching' in the second. The computationally influenced language helps little and contrasts sharply with previous chapters offering more concrete explanations at the physiological and ecological level.

A similar developmental story to that of songbird vocal development is presented by Kuhl in her review of the development of speech perception in human infants. Exposure to the mother tongue *reduces* the capacity of phonetic discrimination in infants so that they end up exhibiting the typical discriminations of their linguistic community. For instance, 7-month American and Japanese infants are able to discriminate between the phonetic units /r/ and /l/ but at the end of 10 months the categories are clearly separated for Americans and conflated for Japanese, showing that language has already altered perception at the time when the first words are uttered. This she explains in terms of "magnetic" effects in categorical perception and the corresponding clustering of categories in combination with the statistics of the first language and 'critical periods' after which plasticity is reduced. Interestingly, she tries to interpret the existence of critical periods in terms of the commitment of neural structures in combination with the local properties of the language community. Once certain neural tissue is used in 'categorizing' the features of the local tongue, it may become progressively harder to change this existing structure —hence critical periods. Unfortunately, this argument *assumes* progressive limitations to neural plasticity and does not explain them. Why would it be harder to re-commit neural tissue to a different language when the adult human brain can be so plastic in other complex tasks such as adaptation to sensorimotor disruptions? The question of the origin of critical periods remains unanswered and would probably benefit also from some form of evolutionary modelling, even if pitched at a rather abstract level.

Whereas human speech development seems more similar to vocal development in birdsongs and less similar to communicative development in more closely related species, this may be a consequence of the narrow focus of the existing evidence which concentrates only on the development of signal production.

Seyfarth and Cheney review the development of signal production, usage, and response in vervet monkeys and cross-fostered Japanese and rhesus macaques. According to them, there are more similarities between humans and other primates when the development of signal usage and response is also considered.

Chapters in the last part of the book on the evolution of communication address a wider range of matters — even, occasionally, the evolution of communication. In fact only five of the nine chapters in this part are really about evolution. The remaining ones either belong in other parts or are unclassifiable.

For instance, Matsuzawa presents a very interesting review on tool use in chimpanzees, which is nevertheless rather misplaced since it is not about evolution, nor even about communication. The author misses a few good opportunities to comment on the similarities between certain uses of tools in social contexts and traditional forms of communication, particularly since most animal (and even human) communication is performative in character (i.e., its end is the concretion of an immediate act as in "Pass the salt, please"), and so a certain *kind* of tool. Cheney and Seyfarth intriguingly entitle their paper in this section "Mechanisms underlying vocalization in nonhuman primates" and make not a single mention of mechanisms, but rather indulge in speculation about the intentional character of human language and evaluate the lack of evidence for similarly intentional uses of primate vocalizations in playback experiments in vervet monkeys. After reading this chapter, full of unsubstantiated claims, one is left with the question of what has been achieved with respect to the evolution of communication. A similar fault is found in Hauser's contribution on brain lateralization in the case of face and acoustic signal perception and expression in apes and monkeys. The evidence in this case is interesting, but little is said about its evolutionary significance. Is lateralization adaptively beneficial? Does it prompt the evolution of further complexity and asymmetries? Does it in any way help us understand human lateralization? Also failing to deal with evolution beyond the odd passing comment is the chapter by Wyttenbach and Hoy on categorical perception in Polynesian field crickets who show basically two behavioural responses (positive and negative phonotaxis) to a continuum of signal frequencies.

Of the contributions that do concern themselves with evolution, two are attempts at phylogenetic reconstruction. In one of the few chapters concentrating on an atypical modality, Hopkins explores electric communication in African mormyriform fish. These fish use pulse- or wave-like electrical discharges that vary in rhythm and shape, and decay with the cube of the distance and are apparently used for advertising purposes. Hopkins does an impressive job in phylogenetic reconstruction by studying the shape of the discharge and the anatomy of the electric organ in related species. However, the chapter is somewhat disappointing since, for such an uncommon modality, little is said about the actual interaction of individuals during communication and its functionality.

From a modelling point of view, perhaps the most interesting chapter in the book is by Ryan and Rand who review studies on the phylogeny of the mate recognition calls of Túngara frogs in Central America. Males can increase the quality of their calls by adding a series of suffixes for which females show a preference. The cost of the suffixes is apparently an increased risk of predation by bats. However, related neighbouring species do not perform this trick. A series of interspecific experiments show that females of these other species also prefer calls with suffixes, suggesting that their evolution is a case of sensory exploitation and at the same time casting some doubts on the handicap interpretation. To further test this hypothesis, the authors reconstruct the most plausible evolutionary tree leading to current species and build the acoustic features of the ancestral calls in the most parsimonious way using existing calls. Females find it difficult to discriminate between conspecific calls and those of the most recent 'ancestor'. The reconstruction is further tested by using an evolved neural network model. In one experiment, selecting networks to recognize the Túngara frog call results in similar responses to heterospecifics as in the case of real females, thus supporting the hypotheses of hidden female biases. In another experiment, neural networks are progressively evolved in the recognition of ancestral calls using the best estimate of ancestry and then compared with networks trained using a random history of ancestry. The latter are worse predictors of the actual female response. This very interesting modelling approach begs some questions however. For instance, in what sense is the training history in neural networks repre-

sentative of actual phylogenetic history? Also, even if the most parsimonious history gives better results than a random history, is the former the reconstruction that gives the *best* correlation? Despite these methodological doubts, similar modelling attempts should be encouraged.

Questions also amenable to a modelling approach can be found in the remaining three chapters. Searcy and Nowicki address the topic of functional significance in song variation in song sparrows by identifying variability in song structure at three levels: within the same individual, between individuals, and between populations. Related to this topic are the rare cases of reproductive character displacement reviewed by Gerhardt. In some frog species in southwestern Australia geographic divergence within a species may occur both in signals and receiver selectivity because habitat overlap with similar species favours some form of differentiation in order to avoid mismating. This effect could eventually be the source of genetic differentiation between the populations in the areas of sympatry and allopatry. Finally, Bass, Bodnar and Marcharterre present an integrative approach to character evolution by considering its structural, behavioural and ecological aspects or dimensions with particular application to the vocal communication system of the plainfin midshipman fish.

As expected from a lengthy volume of twenty four chapters, the quality of the contributions is highly varied. However, except for the misplacement of chapters in the last part, the organisation of the book is sound, and most of the reviews are interesting and quite up-to-date. From a modelling perspective the book is mainly informative about things that could be done and the chapters by Michelsen or by Ryan and Rand show the way for the case of robotics and evolutionary neural network modelling respectively. But it also provides good examples of an integrative ethological approach at work, blending ideas and techniques of genetics, neurophysiology, ecology, and evolution. Perhaps the only general disappointment worth mentioning is that there is little in this book that would lead the reader to suspect that animal communication is a particularly exciting field in ethology. A similar book could have been written, say, about aquatic locomotion. And yet, there is a special fascination about animal communication because of its relationship to themes such as animal intelligence, the problems of conflict and integration of social structures, the evolution of honesty and cooperation, the evolution of human language, etc. Although implicit in many of the contributions, the book would have benefited if this special fascination had been presented in a more engaging manner.