Special Issue: Social Evolution
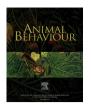
How sociality shapes the brain, behaviour and cognition

In 1838, more than 20 years before the publication of *The Origin of Species*, Charles Darwin began to realize that his theory of evolution by natural selection — originally formulated to explain differences in morphology like the beak of a finch — could also be applied to the evolution of the brain and cognition. After all, he reasoned, thoughts and instincts come from the mind, and the mind can be studied like any other biological trait. It should differ in different species, reflecting the particular adaptations of each, and it can change gradually over time, being transmitted from one generation to the next. In his *M Notebook* (M for metaphysics) Darwin wrote: 'We can thus trace causation of thought … [it] obeys [the] same laws as other parts of structure' (Darwin, 1838, cited in Barrett, Gautrey, Herbert, Kohn, & Smith, 1987, page 543: for Darwin's other thoughts on the evolution of mind, see Barrett et al., 1987).

For many group-living species, some of the strongest selection pressures acting on the brain and cognition come from the social environment: from the need to distinguish different individuals, remember past interactions and predict other animals' behaviour. The results of selection acting within the social domain are ubiquitous: frogs, fish and birds have brains that are particularly sensitive to their own species' calls; monkeys have brain areas that are specialized for the recognition of faces, voices, gaze direction, and for the assessment of other individuals' intention to perform a specific action. Long-lived animals like hyaenas, dolphins, baboons and chimpanzees also recognize the close social relationships that exist among other individuals, perhaps because this knowledge is necessary to predict behaviour and predicting behaviour is necessary for survival and reproduction.

The goal of this symposium is to review what we know about the ways in which evolution acting within the social environment has shaped the brain, behaviour and cognition in different species. To do this, we have brought together field biologists studying species that range from fish to birds to dolphins, monkeys and apes as well as three behavioural neuroscientists who are integrating studies of social behaviour with physiological work on brain mechanisms.

The symposium is dedicated to Peter Marler (Fig. 1), a founding member of the Animal Behavior Society who died on 5 July 2014 at the age of 86. Peter belonged to the 'second generation' of ethologists: students of the founding fathers Konrad Lorenz, Niko Tinbergen, Karl von Frisch and W.H. Thorpe, who carried on and spread this new discipline throughout Europe and North America.

Peter was a giant in our field who combined intellectual energy, insatiable curiosity and a knack for creative, original experimentation. He brought to ethology a perspective that combined evolution with the study of underlying mechanisms. In his research on birds,

for example, Peter did not spend much time worrying about why some species were monogamous and others polygynous — a question that was central to behavioural ecology. Instead, he took different species' mating systems as given and focused his energies on the mechanisms underlying song learning in different circumstances, and on what these mechanisms might reveal about the ways in which evolution had shaped the brain's role in communication. Evolution provided the backdrop for Peter's work, but his heart was in the mechanisms: behavioural, developmental, hormonal and neural.

Peter's focus on communication, ontogeny and the brain, in both birds and primates, brought him into direct contact with the revolution in neurobiology, psychology, linguistics and cognitive science. Among the many scientific questions that attracted his interest were questions about how animals perceive the world, acquire information from it, and act on what they have learned. He saw this problem in large part as one of classification. As they go about their daily lives, animals encounter many stimuli, no two of which are exactly alike. Yet some stimuli are essentially the same and require the same response, whereas others are different and require a different response. How does the animal know when to lump and
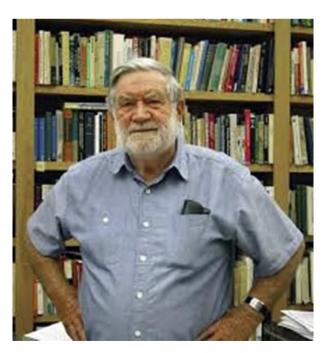
Figure 1. Peter Marler. Reprinted with permission of his family.

when to split? How does its memory, and the information stored therein, affect its response of the moment (Marler, 1982)?

Peter was thinking particularly of social animals, and of questions like 'How does a song sparrow decide that two songs are alike in one respect, since they come from the same individual, but different in another respect, since they constitute different components of the caller's repertoire?' For Peter, 'the means by which organisms achieve satisfactory classifications of things happening around them seems to me, as a biologist, to be utterly mysterious' (Marler, 1982, page 87).

And yet, as so often happened in his scientific work, Peter not only posed the question but also provided an answer. 'To my mind, no organism could possibly deal with this problem efficiently without possessing a virtual battery of innate predispositions, designed to generate natural categories in adulthood. Thus the question is not do natural categories exist but what are they like, how do they differ from species to species, and how can we make sense of the ways in which they develop' (Marler, 1982, page 88). For Peter, therefore, the question of natural categories was in essence a question of how evolution has shaped perception and cognition — how evolution has shaped the way animals think. Which brings us, via Darwin and Marler, to the topic of this symposium: how the evolution of sociality has shaped the brain, behaviour and cognition.

The Social Environment

In the first half of the 20th century, animal cognition was studied almost exclusively in the laboratory, with single individuals as subjects and objects of various sorts as test stimuli (reviewed in: Gallistel, 1990; Gleitman, Fridlund, & Reisberg, 2004; Tomasello & Call, 1997). With the growth of ethology and the proliferation of field studies in the 1950s, 60s and 70s, however, it became increasingly clear that many animals live in complex social environments, and that laboratory studies had failed to consider one class of stimuli that had played an important role in shaping the evolution of animal cognition: other animals. Struck by the apparent complexity of primate societies, Jolly (1966) and Humphrey (1976) proposed that the demands imposed by life in a complex social world have been driving forces in the evolution of primate cognition. They were the first to present what has now become known as the social intelligence hypothesis, which argues that, in order to survive and reproduce, an animal must be able to recognize others as individuals, understand their social relationships and predict their behaviour. Many of the authors in this symposium review research on the knowledge that fish, birds and mammals acquire about each other and discuss paths for future research.

The Cognitive Perspective

From the onset of their work, psychologists studying animal learning in the laboratory were struck by the explanatory power of classical and instrumental conditioning. So powerful were these processes that seemingly any behavioural response could be strengthened or weakened through conditioning or reinforcement. Animal 'minds' or thinking were not suitable topics for study because they could not be measured, and in any case the animal mind was largely a *tabula rasa*, shaped entirely by conditioning and with no pre-existing biases or constraints (reviewed in: Boakes, 1984; Roitblat, 1987).

For other scientists, however, learning involved not only a change in behaviour but also the acquisition of knowledge. In fact, animals could acquire information — about objects in their environment, for example — without ostensibly changing their behaviour. Moreover, the knowledge that animals acquired could include information about the properties of objects and events, and these properties could be measured, dissected and compared across species. Each species' mind, as Darwin predicted, was the product of evolution, and each species' cognitive processes ('causation of thought' in Darwin's terms) could be studied scientifically (reviewed in: Cheney & Seyfarth, 2007; Gleitman et al., 2004; Shettleworth, 2010).

Research in subsequent years has combined these two intellectual traditions and provided clear evidence that many animals are born with predispositions to perceive the world in specific ways; that 'simple' learning mechanisms are indeed quite powerful but also more complex than originally thought; and that the mechanisms underlying learning often lead to the acquisition and storage in memory of what can only be described as complex, structured mental representations (e.g. Dickinson, 1980; Gallistel, 1990; Rescorla, 1988; reviewed in Shettleworth, 2010).

Peter Marler's work on the mechanisms that underlie song learning in birds played a major role in these developments. Early in his studies of song sparrows, *Melospiza georgiana*, and swamp sparrows, *Melospiza melodia*, Peter and his colleague Susan Peters provided clear evidence against 'the longstanding premise of classical learning theory that any sensory stimulus can be attached through learning to any arbitrarily chosen response' (Marler & Peters, 1977, page 519). Given equal exposure to the songs of both species, an individual sparrow is strongly predisposed to learn its own species' song. Such learning, moreover, involves more than just a selective response to certain stimuli: the innate biases that shape learning can be very complex. Whereas swamp sparrows are predisposed to learn any song that contains their own species' notes (or syllables), song sparrows are biased to learn any song that contains the higher-order structural features that occur only in its song, like trilled, repeated syllables with a particular tempo (Marler, 1990). For Peter, the details of song learning in birds were difficult to explain without assuming that young birds organized auditory stimuli into 'schemata' or 'templates', then stored these structured representations in memory and used them to guide the further development of perception and production (Marler, 1991).

Applying this view of learning and cognition to studies of the social environment, we begin with the fact that group-living animals rarely interact at random. Instead, individuals in species like pinyon jays, elephants, dolphins and nonhuman primates behave differently towards different individuals. These differentiated relationships result in structured, predictable patterns of behaviour: good examples are linear dominance hierarchies, subgroups of genetically related individuals, or temporary pair bonds.

Do individuals recognize these relationships? Can they take a nonegocentric perspective, step outside their own world, and gain information from observing others? Is their knowledge of the social environment organized into a structure, much like a Euclidean map includes relational information not just about ego's own location but also about the placement of landmarks relative to each other (Weiner et al., 2011)?

Studies of nonhuman primates were perhaps the first to show that individual animals recognize the relationships that exist among others (e.g. Cheney & Seyfarth, 1980, 1999; Judge, 1982; Silk, 1999), but widespread interest in the information acquired through 'eavesdropping' grew dramatically after the publication of McGregor's (2005) edited book *Animal Communication Networks*. In the present symposium, Bergman and Beehner (2015), Connor (2015), Fernald (2015), Holekamp, Dantzer, Stricker, Yoshida, and Benson-Amran (2015), and Seyfarth and Cheney (2015) review research on animals' knowledge of their social companions in primates, dolphins, hyaenas and fish. Wang, Brennan, Lachlan, and Chittka (2015) show how one individual's decision making affects

another's in a colour discrimination task. Taken together, their results suggest that there is no simple relationship between skills in social cognition, brain size, or the degree of a group's complexity as measured by the number of differentiated relationships. Although we may be able to quantify degrees of complexity in social cognition (Bergman & Beehner, 2015; Seyfarth & Cheney, 2015), cognitive complexity is not limited to those with large brains (Cummings, 2015; Fernald, 2015; Wang et al., 2015), nor does it invariably appear in societies with highly differentiated relationships (Bergman & Beehner, 2015). Building on evidence that the formation of strong, enduring social bonds can affect fitness (e.g. Silk et al., 2010), and the suggestion that to form such bonds one needs to know about other animals' relationships (Cheney & Seyfarth, 2007), Brent (2015) reviews new techniques and some important results in the analysis of social networks that may, in future, allow observers to link knowledge of other animals' relationships with fitness.

Social Behaviour and the Flexible Genome

For many years geneticists pictured individuals as relatively stable entities. Each of us is born with DNA inherited from our parents, and this DNA remains unchanged throughout our lives, regardless of the environment in which we live. This image of the stability and impermeability of the genome, however, has been challenged by a growing body of evidence that the environment — particularly the social environment — can alter how genes work. Consider, for example, the behaviour of male zebra finches, *Taeniopygia guttata*, who sing both to compete with rival males and to attract females. When one male hears another male singing, this causes the expression of an immediate early gene, *egr1*, which would otherwise be inactive. The gene expression is not just part of a general auditory response, because it is not elicited by pure tones or white noise: it is specific to the song of another male zebra finch. And not just any male will do: gene activation depends on the relationship that the listener has with the other male: if the listener knows the other male and has heard him before, the *egr1* response is much weaker; if it is a new male, the response is much stronger. And when the male himself sings, the pattern of neural activity in different brain areas differs depending upon whether the male is singing alone, to a rival male, or to a female (Dong & Clayton, 2008; Jarvis, Scharff, Grossman, Ramos, & Nottebohm, 1998; Mello, Vicario, & Clayton, 1992).

These studies demonstrate that a complete understanding of behaviour, including genetics and physiology, requires a rich, social perspective. To understand what makes a bird sing, you cannot just study an individual in isolation: you have got to know about its species' social organization, how song functions under natural conditions, who the male is singing to, and the history of his interactions with that particular individual. Good genetics and neuroscience require good ethology. Fernald (2015), Cummings (2015) and Watson et al. (2015) highlight recent results in their research on the social genetics and genomics of fish and monkeys.

Information as a causal agent

A common theme running through all of the symposium papers is that, just as selection has favoured skills in learning and memory outside the social domain, selection has favoured skills in the perception of other animals' relationships because these skills increase fitness. In a striking demonstration of the importance of eavesdropping, Fernald reviews evidence that the acquisition of social information alone, even in the absence of any overt behavioural responses, can affect crucial neural circuits and patterns of gene expression in fish (Fernald & Maruska, 2012). Identifying the signal

pathways, moreover, has important implications for studies of sociality, the brain and cognition, and for understanding what we, like Peter Marler, mean when we talk about a 'template' or 'mental representation'. Finally, the idea that information by itself can have significant behavioural and physiological effects has major implications for clinical research on humans. Compare, for example, what Slavich and Cole (2013, page 341) conclude about human clinical studies with what Desjardins, Klausner, and Fernald (2010, page 21176) wrote several years earlier about fish: On humans: '…subjective perceptions of the external social environment (e.g. as being friendly versus being hostile) appear to be more strongly related to genome-wide transcriptional shifts than the actual social—environmental conditions themselves'. On fish: '… social information alone, independent of social interactions, activates specific brain regions that differ significantly depending on what the female sees'.

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Guest Editors