



ELSEVIER

Neurobiology of behaviour

Editorial overview

Mark Konishi and Randolph Menzel

Current Opinion in Neurobiology 2003, 13:707–709

0959-4388/\$ – see front matter

© 2003 Elsevier Ltd. All rights reserved.

DOI 10.1016/j.conb.2003.11.003

Mark Konishi

California Institute of Technology, Division of Biology, 216-76, Pasadena, California 91125, USA

e-mail: konishim@caltech.edu

The main theme of the Konishi laboratory is neuroethology, which is the neurobiological study of natural behavior such as prey capture by owls and singing in songbirds. This approach requires close integration between behavioral and neurophysiological or neuroanatomical studies.

Randolf Menzel

Freie Universität Berlin, Fachbereich Biologie, Chemie, Pharmazie, Institut für Biologie, Neurobiologie, Königin-Luise-Str. 28/30 D-14195 Berlin, Germany

e-mail: menzel@neurobiologie.fu-berlin.de

Our research group applies a top-down approach with the aim of understanding the neural and cellular basis of sensory perception (olfactory, visual), learning, and memory in honeybees. We chose the honeybee because it learns fast and effectively at the feeding site and, under constraint, in laboratory conditioning. We try to relate the various levels of analysis to each other by asking the same questions at the behavioral, neural, cellular, and molecular level.

Introduction

The neurobiology of behavior covers all aspects of neural mechanisms that control behavior. It is neither the techniques nor the level of analysis but the emphasis on behavior that distinguishes this field from other fields of neuroscience. Both intracellular studies of single neurons and the behavioral level of analysis are necessary for understanding behavior. Reflecting this characterization of the field, the present issue contains topics ranging from the neural basis of operant conditioning in mollusks to avian behavior that occurs every twelve months. We selected the topics partly because of our interest and expertise in them and partly because of the emphasis on behavior in the chosen subjects. The animal groups that have been prominent in the study of neural mechanisms of natural behavior include mollusks, insects, electric fish, songbirds, and bats. Nematodes and barn owls can be added to this list, but studies on them have been reviewed in recent years [1,2]. The first group of animals is attractive for the study of brain and behavior, because the neural substrates for their distinct behavior are known. The same genes control the development of organs such as legs in *Drosophila* and vertebrates. Such rules of body organization might even apply to behavior. The best example of this is that the same genes control circadian rhythm in many different animals. Aggression and sophisticated learning in invertebrates are interesting from a genetic point of view too. Finally, we picked the circannual rhythm, because we should learn how the brain controls such long-term behavioral events.

Learning to act in invertebrates

Animals with small and large brains make predictions about the outcome of their actions based on earlier experience with such actions. Mechanistic analysis of operant learning is difficult because such learning, memory storage and retrieval requires an active animal, which is not suitable for intracellular recording. As Brembs points out in this issue, such restrictions can be overcome by two strategies: manipulating single genes and their expression patterns in *Drosophila* and stepwise reduction of the complexity of spontaneous behavior in gastropods. *Drosophila* exposed to pleasant and unpleasant temperatures makes decisions in favor of the more comfortable temperature and relates to these decisions in planning its path. As so much is known about the cellular and molecular mechanisms of classical conditioning in *Drosophila*, one can ask whether classical and instrumental conditioning share the same mechanisms. The expression of the ignorant gene (*ign*) affects these two forms of learning differently, and the mushroom body — known to be necessary for olfactory conditioning — plays no role in visual or ideothetic operant learning. The water slugs *Aplysia* and *Lymnaea* adapt their feeding behavior to rewarding or punishing contingencies. In *Aplysia*, operant reward learning can be studied in the isolated nervous system because the rhythmic activity of the feeding circuit continues to operate and adapts to contingent stimulation of the esophageal nerve. One neuron

(B51), a part of the bite circuit, changes its firing and its cellular properties when the dopamine-mediated reward pathway signals at the appropriate time. Establishing correlations between neural events and behavior is an important first step, but proof of causal relatedness, although difficult to achieve, is a necessary requirement for full understanding.

Navigating between the nest and feeding sites is a common behavior in animals, and insects, with their small brains, are particularly impressive in this respect. In their review, Collett, Graham and Durier focus on one aspect, route learning in ants, and argue that route following initially results from path integration and some fixed responses to dominant landmarks. Only in the course of extended learning during multiple runs along a route do ants appear to associate their path to landmarks in a more flexible way, allowing them when disturbed to correct their runs according to the landmarks. Besides the exciting work currently going on in hippocampus/navigation research in rats and humans [3,4] little is known about the neural mechanisms of spatial learning and navigation — neither in insects nor in other animals. Behavioral experiments are most important in this situation. Is insect navigation restricted to isolated associations between performances (e.g. route directions) and landmarks, or is it based on an integrated representation of spatial relations of learned landmarks? The experiments discussed by Collett *et al.* can not address this question, because they restrict themselves to route learning, but they do also not exclude the possibility of such a rich form of spatial memory.

Talking about integration of multiple forms of behavioral routines, innate and acquired, Giurfa argues in his article in favor of what he calls 'cognitive neuroethology'. His examples come from learning studies in honeybees that focus on the question of whether elemental forms of associative learning may be sufficient to explain the rich forms of behavioral adaptation seen in this insect. Generalizations, concept formation, rule extraction in operant learning, and various forms of configural processing in classical conditioning do not support the notion that this little brain needs to follow a strategy of isolated and dedicated routines. Rather, a cognitive viewpoint should be adopted. Manipulating the structure of the mushroom bodies during the development of an animal allows access to the neural structures potentially involved in configural representations — an enterprise that has just been initiated. An additional approach will be optophysiological and multi-electrode recordings of neural activities in central brain structures in the insect brain during configural processes [5].

Angry little brains

Intraspecific aggression is a common behavioral trait, and its pre-wired neural substrate calls for model studies in

invertebrates. Agonistic behavior comes in many forms, from ritualized displays to fighting, boxing, stinging and biting. Biogenic animals are the common neuromodulators, and as their expression pattern often consists of a small number of well-characterized neurons, the neural substrate of agonistic behavior and its change during intraspecific encounters can be traced neuroanatomically. However, it has not yet been possible to record from these neurons during such encounters. Therefore, specific manipulations of such neurons are required. As pointed out by Kravitz and Huber, *Drosophila* males perform wing threats, they box, tussle, hold on to and chase others, and females lunge with head butting, and fence with the front limb when in an upright or elevated position. The whole battery of *Drosophila* molecular genetics is just in the process of being applied, and it will not be long before it becomes established that *Drosophila* provides an excellent model in aggression research. If it were a social animal we would be even more ready to generalize the expected findings to also apply to other animals and humans, where aggression is a particularly important behavioral trait in social interaction, a trait that can also be addressed in *Drosophila* as there is a social species living on the islands of Hawaii.

Vertebrate neuroethology

Electric fish and bats are two of the most favorable vertebrate groups for integration of behavioral and neurophysiological studies. Electric fish generate and perceive electrical signals. Thus, both the input and output sides of a behavioral system use the same currency, as Zakon points out in this issue. Also, unlike most vertebrate neural systems, the main cellular components of the electrosensory and EOD (electric organ discharge) control circuits have been identified and studied extensively. The level of analysis in this field ranges from social behavior to ion channels. Electrolocation by electric fish resembles echolocation by bats, which is reviewed by Moss and Sinha in this issue. Bats emit calls and perceive echoes returning from prey and other objects. One of the important problems in this behavior is the timing of sound production and processing of information contained in echoes. The authors discuss where and how temporal parameters are encoded in the bat's auditory system and what is known about the premotor areas that control vocalizations. One of the most exciting findings concerns the corticofugal control of neural maps of frequency and echo delays in adult animals by Suga and his associates. The auditory cortex sends modulatory signals to lower-order stations including the inner ear hair cells. The corticofugal control of auditory responses is not unique to bats but has also been shown in other mammals [6].

Birds are another group of vertebrates that have attracted ethologists and neuroethologists. The brain song control system of female birds is rudimentary in species like the zebra finch, in which only males sing. This gender

difference is partly due to programmed cell death in young female finches [7]. However, experimental manipulations of sex hormones and the gonads could neither masculinize the female song system completely nor prevent the differentiation of the male song system. Using gynandromorphic zebra finches in which one side of the body including the brain is male and the other side female, Arnold's laboratory showed that the genetic make up of brain cells and their hormonal environment determine the differentiation of the male brain. The genetic contribution to the brain's gender is not unique to finches but has also been shown in mice by manipulation of the sex chromosomes and the genes for the differentiation of the gonad.

The house sparrow was the first animal in which transplantation of the pineal organ from one individual to the anterior eye chamber of another individual shifted the phase of the circadian rhythm of the recipient to that of the donor [8]. This experiment showed not only that the pineal organ by itself controls the rhythm but also that whatever mediates the rhythm is not carried by the nervous system but by the circulatory system. Menaker and Eskin [9] also reported that the sparrow's call could entrain the circadian rhythm. Apparently, this interesting topic does not appear to have been extensively studied in later years. A recent paper by Levine *et al.* [10] on the effects of group housing on the locomotor circadian rhythm of fruit flies has drawn a renewed attention to the topic. Davidson and Menaker offer a critical view of the work published so far.

Most brain scientists know about circadian rhythms but few know about circannual rhythms. Some of the conspicuous physiological and behavioral events in the life of birds recur at 12 month intervals even under constant light in captivity. Gwinner, using much data from his own laboratories, convincingly argues that the circannual

rhythm is endogenous. Birds accumulate fat and become restless before they embark on annual migration. Some populations of birds contain migrating and non-migrating individuals. Selective breeding of these birds in each generation led to migrating and non-migrating populations after only three generations [11]. The non-migrating birds showed neither fat deposition nor restlessness during the migratory season. This finding lends support to the hypothesis that the circannual rhythm is a heritable trait. The present review is likely to stimulate brain scientists to take this topic seriously.

References and recommended reading

1. Rankin CH: **From gene to identified neuron to behaviour in *Caenorhabditis elegans***. *Nat Rev Genet* 2002, **3**:622-630.
2. Konishi M: **Coding of auditory space**. *Ann Rev Neurosci* 2003, **26**:31-55.
3. Burgess N, Maguire EA, O'Keefe J: **The human hippocampus and spatial and episodic memory**. *Neuron* 2002, **35**:625-641.
4. Ekstrom AD, Kahana MJ, Caplan JB, Fields TA, Isham EA, Newman EL, Fried I: **Cellular networks underlying human spatial navigation**. *Nature* 2003, **425**:184-187.
5. Galizia CG, Menzel R: **Odour perception in honeybees: coding information in glomerular patterns**. *Curr Opin Neurobiol* 2000, **10**:504-510.
6. Sakai M, Suga N: **Centripetal and centrifugal reorganizations of frequency map of the auditory cortex in gerbils**. *Proc Natl Acad Sci USA* 2002, **99**:7108-7112.
7. Konishi M, Akutagawa E: **Neuronal growth, atrophy and death in a sexually dimorphic song nucleus in the zebra finch**. *Nature* 1985, **315**:145-147.
8. Zimmerman NH, Menaker M: **The pineal gland: a pacemaker within the circadian system of the house sparrow**. *Proc Natl Acad Sci USA* 1979, **76**:999-1003.
9. Menaker M, Eskin A: **Entrainment of circadian rhythms by sound in *Passer domesticus***. *Science* 1966, **154**:1579-1581.
10. Levine JD, Funes P, Dowse HB, Hall JC: **Resetting the circadian clock by social experience in *Drosophila melanogaster***. *Science* 2002, **298**:2010-2012.
11. Berthold P: *Bird Migration. Oxford Ornithology Series*. Oxford University Press, Oxford, UK; 1993: 239.