INTRODUCTORY REMARKS TO SYMPOSIUM VIII:

VISUAL ECOLOGY AND NEURAL CODING

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Despite a general agreement that neurons convey information through changes in their electrical activity, the actual code by which this information is represented and transmitted throughout the nervous system still remains elusive. Moreover, most studies on neural coding assess performance on the basis of rather simple stimuli which can be defined by a small number of parameters and which can be varied systematically. Being essential for a system analysis, such stimuli, however, do not allow us to infer what information is encoded by the nervous system under the normal operating conditions of an actively behaving animal.

To understand how nervous systems encode behaviourally relevant information, and to assess the reliability with which neurons represent the visual world, we need to know about the natural conditions in which animals normally operate. Equally, in order to be able to assess the adaptiveness of matched sensory and neural filters, it is necessary to describe and quantify both specific visual habitats and the detection and signal processing requirements of the visual tasks, animals are confronted with.

There is not an easy nor a direct route towards this goal. We can basically envisage two ways of approaching it. On the one hand, neurophysiologists with an interest in ethology try to develop more and more “realistic” ways of interrogating neurons by simulating the naturally occurring input situation or by recording from freely behaving animals in a more or less natural setting. Ethologist with an interest in neural mechanisms, on the other hand, can only do their best to interpret behaviour in terms of the neural processing requirements which are possibly involved in controlling and guiding an animal in its natural environment.

Recent years have seen a number of new developments both conceptual and technical which promise to bridge the gap between our neurophysiological and our ethological knowledge. In a number of different ways, we begin to acquire the tools to reconstruct the visual environments of animals, by analysing the statistics of natural scenes, by identifying through modelling or through comparative studies the functional significance of spectral and motion sensitivities or by confronting neurons with more and more "realistic" stimuli.

Neural coding

Sensory systems and the neural processing machineries associated with them have long been recognised to selectively filter relevant signals from the environment. Eyes are no exception in that they do not sample the world in a uniform fashion. Light sensitivity, resolving power, spectral and polarization sensitivity all vary across the visual field in many animals, most notably in arthropods, suggesting that the eyes represent filters matched to the probability of significant events in the visual environment (e.g. Land 1989). If we consider neural coding with the phenomenon of matched filters in mind, we can identify at least two types of constraints: (i) There are principal limitations set by the physical nature of light and (ii) there are limits to how reliable the sensory and neural hardware can transmit signals and process them. The physical nature of light imposes constraints with respect to the diameter of lenses and photoreceptors and thus on the spatial resolution an eye of a given size can achieve. Since for a given eye size, the number of photoreceptors is limited, increased resolution in one part of the visual field is only possible at the expense of a lower resolution in other parts. Moreover, since photons emanate randomly from a light source, they have to be "counted" for some time interval before reliable brightness information can be inferred, which limits the dynamical range of visual systems (see e.g. Land 1981). In addition, all neuronal processes, such as spike generation or synaptic transmission, are inherently noisy, which limits the information capacity of neurons. Most likely because of this limitation, the spatio-temporal filter characteristics of the peripheral visual system remove large parts of redundant information in the incoming signal, leaving the visual pathway to transmit only those bits of information which are potentially meaningful (Srinivasan et al. 1990; van Hateren 1992)

A crucial aspect of neural coding which has been widely discussed during recent years concerns the time scale on which information is represented by nervous systems. The question is whether the precise timing of individual action potentials is actually important for information transfer or whether relevant information is conveyed only by the mean spike rate within some extended time interval (Perkel & Bullock 1968; Shadlen & Newsome 1994, 1995; Softky 1995; Rieke et al. 1997). Obviously, the first possibility offers a large information transfer capacity and, thus, is attractive from a computational point of view. However, how accurately nerve cells are able to represent sensory information on a fine time scale is limited by the variability of neuronal responses. When a given stimulus is presented repeatedly to a neuron, its responses are by no means identical. It is not uncommon for visual interneurons that the variance of these stochastic neuronal response fluctuations is almost as large as the average response amplitude (e.g. Tolhurst et al. 1983; Vogels et al. 1989; Britten et al. 1993). Of course, the absolute noise level is not very informative on its own. In order to understand the significance of noise for neural coding, the noise has to be related to the stimulus-induced response component as it occurs in the normal situation of a behaving animal. Owing to methodological limitations, there are only few attempts, so far, where the precision of neural coding has been analysed with stimuli possessing in this sense natural and animal-relevant dynamics (Warzecha & Egelhaaf 1997).

Visual ecology

The questions surrounding the significance of noise, the dynamics of naturally occurring input and the type of information actually processed by neurons, which arise when we try to understand neural coding, would seem to strongly motivate the search for ways of quantifying the natural operating conditions of visual systems. Although individual properties of visual systems have been recognized to be matched to the visual environment in which they operate, we rarely have a comprehensive knowledge of the specific visual worlds of different animal species. There are many examples in which some aspects of the visual ecology of animals have been described. However, these descriptions are patchy in the sense that we can in no case document the relevant information of an animal's visual world. By necessity, analysis has focused on general aspects, such as the ambient light intensity, or the spectral distribution of light in the environment and attempts to examine possible causal relationships between the spatial and spectral properties of the environment and the neural processing strategies employed by animals have mostly focussed on the general conditions in different light environments (e.g. Lythgoe & Partridge 1991, Endler 1993, Warrant et al. 1996), on global scene statistics (e.g. Laughlin 1983, Field 1994, Osorio & Bossomaier 1992, Olshausen & Field 1996) or on isolated tasks like foraging in frugivorous primates (e.g. Osorio & Vorobyev 1996), coevolution of flower colours and spectral sensitivity of insect pollinators (e.g. Chittka 1996, Chittka & Menzel 1992), the role of animal colour patterns in communication (e.g. Endler & Théry 1996) and the tuning of the dynamical properties of photoreceptors and motion-sensitive neurons to the particular lifestyle of different insect species (Laughlin & Weckström 1993; O'Carroll et al. 1996). Little is known, however, about the relevant information available in natural scenes from the viewpoint of specific animals. Luminance contrast, spectral composition, reflection and skylight polarisation, and environmental motion are all likely to both provide important cues and set constraints for visual processing, but sofar have not been fully described for any species.

Outlook

Our unfairly short and by no means comprehensive review above is meant to argrue that although we have many isolated pieces of evidence relating neuron properties to the detection and discrimination tasks animals are confronted with, it remains to be seen how well we can integrate the pieces of the jigsaw puzzle into a coherent picture of how neural operations are adapted to naturally prevailing conditions. To be able to view neural coding in the light of visual ecology we need to learn more about how animals move in their natural settings, about the spatial distribution of luminance, spectral, and polarisation contrast in the visual environment they inhabit, and most important of all, about which of the available signals actually provide relevant information to an animal. The biggest technical challenge will be to find ways of analysing neural signalling and its reliability under real life conditions. After all, it is only in this situation that sensory receptors and neurons have evolved, and that their properties are often continuously modified and fine-tuned throughout the lifetime of an animal.

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