SENSORY PHYSIOLOGY AND BEHAVIOR

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Preface

In a recent book Arthur Koestler describes very cynically the superfluity of scientific meetings. He lists the various gatherings that are going to take place in one brief summer season in the Kongresshaus of a small Swiss village, ending the long list with three interdisciplinary symposia, titles of which contain the three words "Environment", "Pollution", and "Future" in three different permutations. By the same token, Koestler could list endlessly meetings on sensory physiology and behaviour or their synonyms, which have taken place all over the world on the national or international level in recent years.

The organizing committee of the Oholo conferences was very well aware of this situation when the topic for the 19th Conference was selected. However this field is relatively new in Israel - only in the last decade were several teams established in this country to carry out combined studies on sensory physiology and behaviour. They attracted ever-increasing numbers of students of zoology, physiology, medicine and psychology. The committee thought that the time was ripe to bring the Israeli students and scientists together with noted investigators from all over the world, to discuss and analyse the state of the art.

The Conference dealt with processing of information obtained through the various senses: visual, auditory, tactile, as well as the olfactory and gastatory senses.

More complex behavioural patterns were also analysed.

No attempt was made to relate these findings to human behaviour, although the act of terror which took place in Maalot, the site of this Conference, only several weeks after the meeting, may call for better understanding of human behaviour. We would like to perpetuate in this volume the memory of the 20 innocent schoolchildren who were killed in Maalot in May, 1974.

The editors gladly take this opportunity of expressing their thanks to the members of the program and organizing committees for their devoted work; to the members of the staff of the Israel Institute for Biological Research who gave so freely of their time, both outside and inside working hours; and to Mrs. Helen Bar-Lev for her skilled technical preparation of the manuscript of this book for printing.

No less thanks go to the participants, those from Israel and our guests from abroad, for making the Conference such a memorable and stimulating occasion. We especially are grateful to the Sessions Chairmen and the Moderator of the Round Table discussion.

We also wish to thank the management and staff of the Guest House at Maalot for their hospitality and care.

Finally, we are greatly indebted to the U.S. Army, European Research Office, for a grant in support of this Meeting.

Rachel Galun,
On behalf of the Editors

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SENSORY PHYSIOLOGY AND BEHAVIOR

WELCOMING ADDRESS

Amnon Ben-David

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It gives me great pleasure to welcome the participants from Israel and abroad to this our 19th OHOLO Conference of 1973. After the tragic event of October, which for some time put in doubt whether we would be able to hold the Meeting, it gives me particular pleasure that we are gathered together here.

The OHOLO Conferences are intended to promote interdisciplinary understanding in specific fields in the forefront of scientific advance, by bringing together our local scientists and distinguished colleagues from abroad.

Our quiet and peaceful surroundings, be it the shores of Lake Kinnereth where our meetings were originally held at the OHOLO Education and Conference Center, or the mountain air of Galilee, here at Ma'alot, provide a relaxed atmosphere for informal discussion which has always contributed to the success of our annual OHOLO Conferences, initiated in 1954.

Our topic this year - SENSORY PHYSIOLOGY and BEHAVIOR - could occupy physiologists and behavioral scientists for much longer than three days of discussions. We hope that we can cover in the time as our disposal enough aspects of the topic as to bring them into sharper focus and perhaps awaken new ideas for future endeavours.

I hope that we shall have a pleasant and successful Meeting.

DEVELOPMENTAL PLASTICITY IN THE CAT'S VISUAL CORTEX

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FEATURE DETECTION IN VISUAL SYSTEMS

In many species, the processing of visual information reaches a high level of complexity right in the retina itself. In rabbits (Levick, 1967), pigeons (Maturana and Frenk, 1963) and frogs (Lettvin, Maturana, McCulloch and Pitts, 1959), for example, retinal ganglion cells often demonstrate remarkable stimulus specificity. Within its receptive field (the region of receptors from which it receives information) each cell may require a quite specific visual stimulus to coax it into responding. Ganglion cells in these species sometimes require an edge at a particular orientation, an object moving in a particular direction or at a particular velocity, or even the complete absence of any pattern in the field, in order to make them respond.

Notably, those species with complex retinae have laterally placed eyes with rather little binocular overlap of the visual fields of the two eyes; but in cats and monkeys (with their frontal eyes and enormous binocular field) complex image processing seems largely to be delayed until the visual cortex - the first site in the geniculostriate pathway at which most neurones receive signals from both eyes. While the majority of ganglion cells and neurones of the lateral geniculate nucleus have straightforward round receptive fields with antagonistic surrounds (which only demand localized illumination or darkening), cortical neurones are almost always orientation-selective; they only respond when an edge or bar of a particular orientation appears in the receptive field (Hubel and Wiesel, 1962, 1968). The majority of them also have input from both eyes and it seems reasonable to suppose that image processing is delayed until the combination of simple messages from the two retinae, which are both viewing the same object in space.

Several workers have suggested, and provided evidence, that binocular cortical neurones in cats and monkeys play a part in stereoscopic vision (Barlow, Blakemore and Pettigrew, 1967; Joshua and Bishop, 1970; Hubel and Wiesel, 1970a). Each cell has very similar receptive field properties in the two eyes, but the two fields are not necessarily on exactly corresponding points, there is a limited variable disparity on the two retinae. Most neurones respond much more vigorously if stimulated by appropriate images falling on both receptive fields (as if the animal were viewing a single object at a particular distance from the eyes). The optimal disparity, and therefore the optimal distance, varies from one cell to another and thus the population of neurones may act as a system for the analysis of stereoscopic distance. The efficacy of this remarkable neural apparatus relies on the specific pattern-detecting properties of cortical cells, the similarity of these properties in the two eyes and the exact disparity-selectivity of each cell. Recent experiments have demonstrated that all of these properties are influenced by early visual experience and, indeed, the active modification of neural connections may be responsible for establishing the system for analysing retinal disparity.

DEVELOPMENTAL INFLUENCES IN THE KITTEN'S VISUAL CORTEX

Genetic information alone is adequate to provide the majority of cortical neurones with connections from similar regions of both retinae: in the visual cortex of young kittens that have never had any visual experience, the majority of cells can be influences through both eyes (Hubel and Wiesel, 1963; Wiesel and Hubel, 1965; Barlow and Pettigrew, 1971; Blakemore and Van Sluyters, 1974). However, the receptive fields are diffuse, rarely strictly orientation-selective and never precisely "tuned" for retinal disparity (Pettigrew, 1974; Blakemore and Van Sluyters, in preparation). Visual experience early in life seems to refine crude innate specifications and, indeed, is capable of modifying the properties of cells quite drastically.

While depriving a kitten of patterned visual experience through <u>both</u> eyes simply leads to a general degradation in neuronal responsiveness (Wiesel and Hubel, 1965), covering <u>one</u> eye alone, even if only for a few days, causes virtually all cortical cells to abandon their connections from that eye (Hubel and Wiesel, 1970b). This loss of input occurs only after monocular deprivation between about 3 weeks and 3 months of age, and, within this "sensitive period", the changes are more or less reversed by covering the previously deprived eye and forcing the animal to use its originally inexperienced eye (Blakemore and Van Sluyters, 1974).

Inducing an artificial squint or deviation of one eye (strabismus) by sectioning one of the extraocular muscules of the eye also causes a specific reduction in the proportion of binocularly-driven cells and leaves two populations of neurones, some driven by the squinting eye, the others driven by the normal one (Hubel and Wiesel, 1965). However, small vertical misalignments of the visual axes, induced by rearing kittens wearing goggles with prisms of opposite power in front of the two eyes, can cause a remarkable compensatory change in receptive field organization. The cells usually remain binocular (if the prismatic displacement is not large) but each pair of receptive fields becomes, on average, vertically misaligned as if to correct for the misalignment of the retinal images of objects in space (Shlaer, 1971). Thus, during development, the disparity selectivity of each binocular cell is becoming refined (Pettigrew, 1974), and the optimal disparity may even be adjusted to match the alignment of the visual axes and to the most probable retinal disparity of the images of objects in the outside world.

The orientation selectivity of cortical neurones is also subject to a modifying influence. Kittens reared in conditions that restrict their visual experience more or less to edges of one orientation develop orientation-selective cortical neurones "tuned" almost exclusively to that orientation (Hirsch and Spinnelli, 1971; Blakemore and Cooper, 1970). These "environmental modifications" of orientation selectivity can also only occur as a result of visual stimulation within the 3 week to 3 month sensitive period (Blakemore, 1974) and they require only a few hours of exposure at the peak of this period, during the fourth week (Blakemore and Mitchell, 1973).

Thus, during the first few weeks of life, a number of crucial changes are occurring in the visual system of the kitten. The eyes change their orientation in the orbit and the two visual axes gradually become convergent rather than divergent (Pettigrew, 1974). Orientation selectivity is being refined and even modified as a result of visual experience. The binocularity of cortical cells is stamped in, their disparity selectivity is narrowed and their preferred disparities may even change to match the alignment of the retinal images.

THE POSSIBLE FUNCTION OF ORIENTATIONAL MODIFICATION

It can be contended that environmental modification of preferred orientation would bestow important selective advantages on an animal, since it might match the detection properties of its visual system to the predominant features in its visual world. Indeed, cats reared in environments of one orientation have slight but definite acuity deficits with regard to stimuli of the opposite orientation (Blakemore and Cooper, 1970; Muir and Mitchell, 1973). However there are two important objections to this concept:

1) The acuity deficits produced even by very prolonged exposure are really quite small. It would be difficult to imagine how a subtle change in the population of orientation-detecting neurones (caused by slight differences in the probability of certain orientations in the normal visual environment) could have any noticeable effect on sensitivity or acuity.

2) One could argue that some very important stimuli in an animal's visual world (for instance, the shape of a dangerous predator) are likely to occur very rarely, not very commonly. To lose the ability to detect such stimuli would be disastrous.

There might be an alternative reason for binocular animals to possess the ability to change the preferred orientation of their cortical cells. In order to play their proposed role in the analysis of retinal disparity, these cells must be capable of "recognising" the two images of a single object in the two eyes, in order to signal its disparity. The fact that the optimal orientation of cortical cells is always very similar in the two eyes means that they will only respond optimally when the two images of a single contour (having the same angle on the two retinae) appear on the receptive fields. But it seems an intolerable burden on genetic information alone to specify for each cortical cell exactly what its orientational preference will be, and to ensure that it is virtually identical in the two eyes. However, environmental modification of orientational preference could ensure that both receptive fields of each cortical cell adopt very similar orientations, for the two receptive fields will then be habitually stimulated by the two similarly orientated images of single objects in space.

Thus environmental modification of orientation selectivity, like developmental changes in binocularity and disparity selectivity, may be crucially involved in constructing the neural apparatus involved in stereoscopic vision.

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