

## GENERAL INTRODUCTION

### **Why are there principles of sensory processing?**

Sensory systems share a common purpose. Energy is gathered and transduced by receptors to provide the nervous system with sets of measurements concerning the state of the world. These measurements are processed to extract biologically relevant parameters that can then be used to formulate appropriate behavioural responses. Common purpose is governed by common physical and biological constraints. As a result, sensory systems have evolved similar solutions to operational problems. Some of these solutions are finely illustrated by work on particular organisms, partly because these animals provide favourable material, but ultimately from the efforts of those who have investigated them. The purpose of this meeting was to assemble a variety of studies that demonstrate principles of sensory processing and to suggest comparisons between systems that might further our understanding of sensory processing.

### *Understanding sensory processing*

The study of behaviour defines the sensory information that animals acquire and use. Indeed, the success of the majority of the studies reported here depends upon behavioural work that has defined the sensory process. Outstanding examples of well-defined sensory processes are the jamming avoidance response of electric fish (HEILIGENBERG), echolocation in bats (SUGA) and auditory localization by the barn owl (TAKAHASHI). In these cases a knowledge of the stimulus allows one to specify the computations that are required to execute a well-defined task. This fundamental understanding provides a set of hypotheses for neural function that enables one to design experiments that can identify the function of neurones and pathways. Since one of the first tasks of an experimentalist is to design a stimulus, plausible *a priori* hypotheses are invaluable.

Other sensory tasks have proved less easy to define than echolocation or jamming avoidance. Although colour vision is well accounted for in terms of quantum catches by visual pigments (MOLLON; LYTHGOE & PARTRIDGE), its neural basis is far from resolved. For the chemical senses, for multimodal integration, and for pattern recognition in general, we still lack a computational framework, defined from first principles. In these intellectually and technically challenging areas, theories, computational models and observations on neurones and pathways feed off each other in an attempt to formulate and test hypotheses (ROLLS; PERRETT *et al.*). We should be encouraged that a well-defined computational framework has been developed for the visual detection of motion. Moreover, using this framework one can generate plausible hypotheses of neural function (KOCH, WANG & MATHUR). Psychophysicists interested in pattern

recognition should take heart from the fact that, as for colour vision, the computational approach to motion detection had its origins in the study of behaviour (Hassenstein & Reichardt, 1956). Comparative physiologists, who were well represented at this meeting, will point out that the animal studied was a beetle.

Contrary to what has just been said, the study of insect vision suggests that exact theoretical solutions to problems of sensory computation can be misleading. Ants and bees determine the sun's position from small fragments of the celestial polarization pattern. Arguing from first principles, one might easily conclude that this task is a difficult pattern-recognition problem, involving spherical trigonometry. In fact, these insects use a mathematically inexact but operationally accurate approximation that provides an extraordinarily simple but effective solution (WEHNER). To understand sensory processing one should not only travel the high road of exact theory but also explore the short cuts.

Nor should we view sensory coding in purely sensory terms. Ultimately, sensory systems must progress to motor systems. The mammalian superior colliculus offers an outstanding opportunity to study the transfer of information from sensory to motor coordinates (SPARKS). In the jamming avoidance system of electric fish (HEILIGENBERG) the motor control is relatively simple (oscillate faster or slower) and so, it seems, is the sensory-motor interface. For the reflex control of limb position in locusts, two types of interneurone intervene between sensory receptors and motor neurones (BURROWS). These cells have well-defined sensory receptive fields and motor projections. They also show the basic patterns of convergence, divergence and lateral inhibition typical of sensory systems, but they are not arranged in spatially explicit sensory or motor maps. Such cells cannot be viewed solely in sensory or motor terms. Viewed as a sensory-motor network, this system may provide clues to the operational principles that govern the integration of sensory and motor pathways. On this same theme, and at a slightly higher level of complexity, descending interneurons in the locust (ROWELL) detect course deviation during flight from patterns of convergent polysensory input in the head. However, neither these descending cells, nor the motor system they instruct, explicitly code the familiar axes of yaw, pitch and roll. The locust has constructed its own coordinate systems for coding without regard to Euclid, and these may be related as much to motor correlates as to sensory ones. Sensory processing may often be contingent upon particular motor activities. For example, signals from bat-detecting auditory neurones need only be transmitted to flight neurones while a cricket is flying (HOY, NOLAN & BRODFUEHRER). Behaviour, and hence processing, takes into account the previous history of stimulation and action and this is well illustrated by habituation and satiation in the coding and processing of taste (ROLLS).

Sensory-motor interactions are not confined to the nervous system. Motor output alters an animal's position and surroundings, so producing reafferent sensory signals. When reafference is reliable, the motor commands themselves can be used to predict sensory inflow. Indeed, in highly predictable situations, such as

eye movements, motor command (efference copy) can substitute for sensory feedback (SPARKS). Mormyrid electric fish make remarkable use of motor commands (BELL). A corollary discharge, originating from the motor command centre driving the electric organ, acts in all three subdivisions of the electrosensory pathway. In two pathways the corollary discharge obliterates the signal generated by the electric organ's discharge, to facilitate the detection of the signals produced by other organisms. These corollary discharge effects are surprisingly finely tuned, one by means of appropriate conduction velocities, and the other by means of an 'expectation generator' that predicts the reafferent signal on the basis of past experience. The third pathway is sensitized by corollary discharge to assist in active electrolocation.

By placing mechanisms within a functional context we raise evolutionary questions. Because a number of visual pigments have been sequenced, the study of the ecological, behavioural and genetic factors associated with the distribution of visual pigments (LYTHGOE & PARTRIDGE; MOLLON) suggests exciting prospects in evolutionary biology. A classical approach to evolution is the study of comparative anatomy. This approach has received considerable impetus from the relatively new methods for tracing pathways and delineating functional subdivisions in the mammalian sensory cortex. This type of comparative study (KAAS) reinforces the existing picture of a continuous elaboration of sensory areas during evolution, but suggests that developmental processes allow for a much greater diversity among species than had previously been envisaged.

#### *A sample of principles*

The principles discussed by the contributors are too numerous and diverse to be concisely reviewed. Here I simply present a sample of principles, many of which were the subject of general discussion at the meeting. This sample is biased by my own interests and perspectives. Nonetheless, it serves to illustrate that there are both similarities between sensory systems, indicating principles, and dissimilarities which help define the conditions under which principles operate.

#### *Matching*

The most familiar principle is the matching of coding to signal. At a molecular level, fish visual pigments are matched to the colour of light in different types of water to maximize sensitivity and contrast. In addition, sets of pigments may be carefully positioned within the spectrum so as to allow an animal to discriminate the widest variety of natural objects on the basis of their colour (LYTHGOE & PARTRIDGE). For many insect eyes, both the optics and neural processing are matched to the statistical properties of natural signals to increase the accuracy of coding (LAUGHLIN). A fine example of matching in a compound eye is the correspondence between the layout of the polarization-sensitive photoreceptors in the bee POL area and the celestial polarization pattern (WEHNER). This array of ultraviolet-sensitive receptors provides a matched filter that solves the sun compass problem by acting as a template. Matching is also observed in animals

that use their sensory systems for communication and active location. As John Lythgoe pointed out in discussion, many bioluminescent deep-sea fish emit blue light and have a blue-sensitive visual pigment, corresponding to the wavelengths that are least attenuated by water. The sensitivity of cricket auditory systems is matched to the frequency of conspecific calls (HOY, NOLAN & BRODFUEHRER). The tuberous electroreceptors of electric fish are tuned to the frequency band occupied by conspecifics (HEILIGENBERG). The auditory system of bats is precisely tuned to its own biosonar signals (SUGA). It was suggested in discussion by Dave Perrett that the principle of matching extends to higher levels. Darwin pointed out that facial expression is an important means of communication in primates. The population of face-recognition neurones in primates (PERRETT *et al.*) can be viewed as a set of filters matched to this biological signal.

There is a simple explanation for many types of matching. With a limited number of cells it pays, in terms of accuracy, to deploy them where you expect the signal to be. Thus matching reduces redundancy, in the sense that it reduces the number of idle cells. Note that matching is not restricted to sensory systems. The motor map of the superior colliculus (SPARKS) uses more neurones to code the more frequent and necessarily more precise small movements than the less frequent and less precise large ones. This observation may be related to the familiar size principle of motor neurone recruitment.

#### *Antagonism, opponency and redundancy reduction*

During sensory processing one component of the stimulus is often subtracted from another. Such antagonistic interactions play a number of roles, as illustrated by lateral inhibition. In the visual system, lateral inhibition enhances the responses to intensity fluctuations by, as Ernst Mach put it, 'effacing the mean'. Lateral interaction also generates useful spatial filters in the mammalian visual system (e.g. KOCH, WANG & MATHUR) and sharpens spatial localization in the Mormyromast system of gymnotid electric fish (BELL). When sound frequency is mapped by lineal position, inhibition sharpens tuning curves by suppressing responses to side bands (SUGA). The receptive fields of interneurones coding mechanosensory inputs from the locust leg exhibit pronounced inhibition that assists in coding the stimulus position (BURROWS). In the fly retina, antagonism removes the unchanging signal component (LAUGHLIN) associated with the mean light level. The elimination of this standing signal reduces the risk of saturation and maintains synaptic operations in the region of highest gain. This observation helps explain why a fine balance between inhibitory and excitatory response components is a property of so many sensory neurones and processes. Moreover, to balance responses at a favourable level, opponency and antagonism often remove those components of the signal that can be predicted from their spatial or temporal context. The removal of the predictable again reduces redundancy, helping a sensory system to make the best use of a limited number of cells. For example, in taste processing, antagonism sharpens neural tuning as one

ascends the neural pathway. By reducing redundancy this sharpening can, in principle, increase the efficiency with which multimodal associations and generalizations are made in simple neural networks (ROLLS). It was noted in discussion that the corollary discharge effects seen in mormyrid electric fish (BELL) also remove redundancy. Corollary discharges remove the reafferent sensory inputs that usually follow motor acts: a predictable and, hence, redundant signal component that can easily saturate sensitive cells. In summary, as argued by Barlow (1986), redundancy reduction is a useful principle, capable of explaining interactions at many levels of sensory processing.

### *Parallel pathways*

The idea that information is channelled into different pathways is in vogue for primate visual pathways. Several authors drew attention to the fact that form, colour and depth plus motion are, to some extent, segregated early in processing. Compelling examples of parallel pathways are provided by the auditory pathways of bats and owls, by electrosensory processing, and by vision in bees. Auditory receptors in the ear code both intensity and timing but, early in processing, these two aspects are dissociated and coded in parallel, converging at a higher level to compute higher-order parameters such as spatial location (SUGA; TAKAHASHI). The division into two pathways may be advantageous because the properties of the neurones required to conserve temporal information differ from those required to code intensity. In electric fish, time is again coded in a separate pathway, divorced from intensity (BELL; HEILIGENBERG), and the 'time' neurones resemble in structure those found in the time pathway of owls. In electric fish the time/intensity division starts at the receptors, emphasizing that parallel pathways originate from the dissimilar filtering of a common input. Ants and bees determine the sun's position with two parallel systems located in different retinal areas. One system is polarization-sensitive and the other colour-sensitive. The photoreceptors of hymenopterans are inherently sensitive to both the wavelength and the plane of polarization of light. In the colour region of the retina the photoreceptors twist to degrade polarization sensitivity, presumably to reduce the possibility that colour and polarization signals interfere with one another. Thus, parallel processing also reduces ambiguities. In summary, parallel pathways are a simple solution to the problem of extracting many different types of information from a large receptor array, such as a retina. This arrangement could also enhance the accuracy of neural coding. The precise coding and processing of one parameter (e.g. timing) may require membrane properties that are incompatible with coding of another parameter. The solution to this cellular problem is a division into separate pathways.

### *Mapping*

There are often orderly arrays of neurones, across which the sensitivity to a stimulus parameter changes systematically. There are retinotopic maps in visual systems (e.g. KAAS; LAUGHLIN), maps of body surface in electric fish

(HEILIGENBERG) and tonotopic maps in the auditory pathways of owls and bats (TAKAHASHI; SUGA). The coordinates of these maps correspond to the coordinates of the receptor surface (retina, skin and cochlea, respectively). Consequently, sceptics can argue that these maps are the product of basic developmental mechanisms and need play little role in facilitating processing. However, the auditory pathways of owls and bats both map parameters that are not explicit on the cochlea, but are computed from separate streams of sensory inflow. Nor are maps limited to purely sensory parameters. The primate inferior colliculus contains a motor command map (SPARKS) in which the locus of neural activity specifies the distance and direction of a saccade. This map does not resemble the distribution of ocular-motor neurones, nor does it always correspond to retinal coordinates. In addition, the motor map derives information from the modalities of sight, touch and hearing. Auditory mapping is dynamic in the sense that when the eyes move and the ears remain stationary, the auditory inputs are adjusted to keep them in register (SPARKS).

Knudsen, du Lac & Esterly (1987) suggest that these computed maps demonstrate that orderly neural arrays simplify processing by bringing cells with similar properties into close proximity. For example, patterns are often extracted from the responses of neurones that are close together in space and a corresponding proximity in the brain will reduce the length of the connections required for the commonest computations, as well as simplifying development. Spatial organization also simplifies higher-order pattern extraction. For example, motion is more readily extracted from a spatial map using a simple set of regularly repeated connections (KOCH, WANG & MATHUR) than from a clump of randomly arranged cells. The distribution of activity across a map may also enhance accuracy by allowing for interpolation or the taking of weighted averages (HEILIGENBERG). Finally, the rules for generating and processing information on one coordinate system can be transferred to another by mapping and processing new sets of inputs according to the same rules.

Although useful, mapping is not essential. In discussion, Hugh Rowell and Ron Hoy both emphasized that maps are conspicuously absent from insect sensory-motor systems. For example, mechanosensory interneurones are not arranged in a map corresponding to the surface of the locust leg (BURROWS). Nonetheless, they map the leg in the strictly mathematical sense that behaviourally relevant patterns of stimulation are represented by unique combinations of neural activity. In discussion, Ron Hoy emphasized that neural processing requires defined networks of interaction, and these exist without spatial mapping. Hugh Rowell proposed that the critical difference between vertebrates and invertebrates may be one of scale. In general, invertebrates have smaller ganglia and fewer neurones are involved in processing. In a smaller system one neurone can, in principle, contact a significant proportion of all other cells, without excessive arborization and lengthy collaterals. Thus, the rules required to generate and operate smaller networks need not involve mapping. To support this argument, insects do have elaborate retinotopic maps in the compound eye. Here a large array of receptors is created

according to a relatively simple set of developmental rules. This extensive array necessitates mapping at higher levels, to facilitate both development and function.

### *Population, ensemble and coarse coding*

The observation that specific patterns of stimulus are represented by the simultaneous activity of many broadly tuned neurones was made repeatedly. The motor map of the superior colliculus demonstrates the principle of population coding (Lee, Rohrer & Sparks, 1988). Although each point on the motor map codes a specific movement, a fairly large patch of cells is activated to elicit a given saccade. It follows that a given neurone in the motor map is activated during a number of different saccades. In this sense each cell is coarsely tuned. Nonetheless, the population of activated cells precisely specifies a saccade. Their summed output corresponds to a vector sum, each vector being specified by the activation of one cell. Since the distribution of activity across the population is symmetrical, the vector sum aligns with the centre of the population. Thus, many broadly tuned cells specify a precise output. Population coding may enhance accuracy and reliability. In large populations, poor resolution at the single-cell level is compatible with accuracy if one is able to average many outputs. For example, the extraordinarily accurate determination of timing involved in the jamming avoidance response is achieved by averaging the outputs of many cells (HEILIGENBERG). As John Mollon pointed out in discussion, human colour vision is coarsely coded, for it depends upon three cone types with widely overlapping sensitivities to the wavelength of light. Nonetheless, a web of neural processing constructs a richly endowed colour sense.

Individual cells with extraordinarily well-tuned responses may also collaborate to represent complex patterns. Even though single face-recognition cells respond to specific features, such as those of an individual, they are likely to be members of an ensemble of similar neurones that allows primates to recognize a wide variety of faces (PERRETT *et al.*). In this regard, it should be noted that ensemble coding is, in many situations, more efficient. Just as words represent many more objects than the 26 letters of the English alphabet, ensembles can code many more patterns than there are constituent cells. Furthermore, representing sensory patterns in groups of neurones can be extremely powerful when combined with associative neural networks (ROLLS), allowing for properties such as the completion of incomplete patterns, and resistance to damage.

### *Conclusion*

This introduction makes a case for there being common principles governing sensory processing in functionally and phylogenetically diverse systems. I would like to thank the participants for drawing many of these principles to my attention (subject to the usual qualification that all mistakes and lapses in critical ability are my own). It is interesting to observe that many of these principles can be related to the accuracy and efficiency of coding. This observation fits in with the idea that animals strive to maximize the return from their investment. One of the ways in

which animals have done this is to reduce redundancy. However, three speakers pointed to duplications in sensory systems that have, to some extent, increased redundancy. Gene duplication (MOLLON) created a new long-wave visual pigment, and sensory pathways and maps appear to have been duplicated, both in the evolution of the mammalian sensory cortex (KAAS) and in electric fish (HEILIGENBERG). In each case, this duplication is seen as an essential step in evolution, creating the potential for change without disrupting existing function. This is the type of argument proposed by Ohno (1970) for gene duplication in general, and his statement that 'natural selection merely modified while redundancy created' may be as true for sensory systems as it is for the genome.

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