The Twelfth Bartlett Memorial Lecture:
The Role of Single Neurons
in the Psychology of Perception

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I feel deeply honoured by your invitation to give the Bartlett lecture, and am especially glad to do so in Holland, the home of so many distinguished psychologists of sensation and perception. And there is a third reason why it has given me much pleasure, for Sir Frederick Bartlett was one of those who had an important influence on the direction of my career some 40 years ago. I had to decide whether to spend my last year at Cambridge reading psychology or physiology, so I attended a short course of introductory lectures he gave in July. About half a dozen of us sat on upright wooden chairs circled around him as he sat in an armchair, smiling benignly. The first thing he did was to tell us to close our notebooks, for he was not going to say anything that would help us to pass any exams. And I believe the very last words of his last lecture were, “So you see it is all very difficult”. I was very glad he said that, for I had in fact found it all very heavy going: my brain seemed always to be lost in clouds of uncertainty when “remembering”, “thinking”, or “perceiving” were mentioned, because there was no conceptual framework for these processes except the words themselves and others spun around them. What I was looking for were the definable quantities of physics, chemistry and even physiology; these I could handle conceptually in their geometric and functional interactions, whereas I always find a purely verbal argument about abstractions difficult to follow and impossible to believe. So this lack of any nonverbal conceptual framework was very painful.

There was one phrase I think I recall him using that particularly aroused my interest—“the effort after meaning”; intuitively this seemed to be very important, but however much effort I made the meaning

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never quite emerged. I had almost decided that my mistrust of words made me unsuited to a career in psychology, but all the same I put my problem about "physiology or psychology" directly to Bartlett. After finding out that I was mainly interested in problems of sensation and perception, he said he thought that E. D. Adrian's research over the last 20 years had made more difference to that subject than any results obtained from within psychology itself.

That was a remarkable thing for a professor of psychology to say, but was he right? It was enough, combined with my trouble with verbal arguments, to tip me into physiology; but was it true then, and is it true now, that physiology provides more insight into the functions of the brain than the psychological approach?

Physiology has provided some answers, which I shall discuss in my lecture, but I shall also return to this question.

From Sensory to Perceptual Neurons

I plan to review rapidly a small fraction of the experimental evidence behind current views on the role of single neurons in perception. E. D. Adrian was famous for many things, but I think the series of discoveries that Bartlett was referring to were on the activity of sensory nerves (Adrian, 1928). Figure 1 shows some early records, obtained with Yngve Zotterman nearly 60 years ago, using a three-stage valve amplifier and a capillary electrometer for recording (Adrian and Zotterman, 1928). You may wonder how any conclusions at all could be drawn from such awful records, but Adrian was a master at doing the simple and elegant controls which established convincingly that they resulted from action potentials in single sensory fibres—in this case coming from muscle spindles in the sterno-cutaneous muscle of the frog. It was obviously a landmark to know that the messages you receive when you prick your finger or taste your wine are composed of these brief electrical pulses travelling in nerve fibres.

Some dozen years later Hartline (1940) was able to record from single optic nerve fibres, and Figure 2 shows one of his results. A single fibre picks up from a large area of the retina, and within this receptive field (or at least the centre of it) the effects of light are effectively summated. This figure shows how a large dim spot produces almost the same response as a small bright one. It was this experiment that got me interested, for the optic nerve fibres carry messages that result from two or three stages of synaptic processing, and I could not believe that retinal ganglion cells did no more than summate the effects of light: Were there not operations on the sensory side analogous to the "integration" that Sherrington had demonstrated in the control of movements? I therefore repeated Hart-

line's experiment and found as he had that the sensitivity rose (threshold fell) as the spot size was increased; but this only held up to a point, and after that the sensitivity decreased. The decreased sensitivity suggested there was inhibition from the surround, and it was possible to demonstrate this inhibition directly (Barlow, 1950, 1953). Hartline (1949) was the first to discover lateral inhibition, in Limulus: had he used larger spots, he would have discovered it in the frog ten years earlier.
I did that repetition of Hartline’s experiment in 1950, when Lorenz and Tinbergen were popularizing the idea of “innate releasing factors”, and I naturally considered the possibility that activation of a frog retinal ganglion cell might release certain forms of behaviour. In fact, I gave a talk to the Experimental Psychology Group, the predecessor of the E.P.S., on “The Psychology of the Frog’s Retina” on July 7, 1952, 32 years ago almost to the day. I concluded that talk by suggesting that the firing of certain neurons in the frog’s retina should be regarded, not as initiating sensation or perception, but practically as orders to execute orienting and snapping responses.

Life is more complicated than it seemed then; Lettvin, Maturana, McCulloch and Pitts (1959) have shown that the frog retina contains more types of ganglion cell than Hartline and I knew about and Ingle,

(1968) and Ewert (1970) have shown that there is more to a frog’s feeding habits than simply responding to the retina’s orders. But I think the idea that a single cell says something psychologically important remains. Lettvin and his colleagues took this up and particularly emphasized the fact that their pattern selectivity was invariant for changes of luminance and contrast: the eye was not so much a detector of light as a detector of patterns created by those objects and events in the environment that were important for the animal.

Hill, Levick and I were looking at the rabbit retina at about this time and finding that it was even more complicated than their account of the frog retina; Figure 3 is a summary (Levick, 1965) showing the receptive fields of retinal ganglion cells that were selective for the direction of motion, speed of motion and orientation of stimuli (Barlow, Hill and Levick, 1964). I am sure that it is not a complete account of all the
different types of cells the rabbit retina contains; for example, colour selective ones, which the rabbit must possess, are not shown because they had not been found. But it certainly shows that different cells are selective for different patterns of excitation, and therefore the rabbit retina performs a primitive form of pattern classification.

Directional selectivity is perhaps the best example to illustrate further. There are very large numbers of these cells covering different parts of the visual field, and in each part there are cells preferring different directions of motion; hence the pattern of activity among the different cells tells the rabbit the direction of movement of objects in the various parts of the visual field. It can easily be demonstrated (Barlow, 1969) that a given cell responds preferentially to one direction of movement despite large changes of mean luminance or contrast, and the contrast can even be reversed without altering this preference. There is also some degree of invariance for position, shown by the fact that a small spot moved to and fro elicits more impulses in the preferred direction over most of the receptive field.

So far I have considered retinal ganglion cells, which are separated from the physical stimulus that acts on the receptors by only two or three synapses. But already they have some of the attributes of perceptions, for they respond to environmental events and objects of importance to the animal, and seem to be strangely insensitive to alterations of the proximal stimulus that are compatible with the environmental event remaining unchanged. These cells must be important as triggers or releasers, simply because they are the cells on the visual pathway mediating these reactions; but are neurons with similar properties important for our own sensory experience and perception? Let us now look at the cortex, which is obviously more relevant for this problem.

Hubel and Wiesel (1962) mapped the receptive fields of simple cells in the cat primary visual cortex, and the prominent new form of selectivity they found was for orientation. In the cat (unlike the rabbit) there seem to be no orientationally selective cells in the input from the retina, most of which have the centre-surround arrangement described by Kuffler (1953). But simple cells in striate cortex have elongated receptive fields, and to excite them optimally an elongated stimulus of appropriate orientation is required. We now know that they are also selective for the size, or spatial frequency content, of the stimulus. Other cells, the "complex" ones, have similar pattern-selective properties, but their receptive fields do not give any hint about the means by which their pattern selectivity is achieved. Hubel and Wiesel suspected that they were fed by simple cells and were thus the first to suggest how a degree of positional invariance could be achieved, but their idea has not stood up well, for complex cells receive a direct input from the L.G.N. This does not rule out all hierarchical models of perception but merely shows that it is not organized in such a simple manner as was originally supposed.

If I knew what part the orientationally selective cells of Hubel and Wiesel played in perception I would say so, but although physiologists often call them bar and edge detectors, I doubt if many of us think they are directly responsible for the perception of bars and edges, any more than we think that the red-sensitive photoreceptors are responsible for the experience of redness. For a physiologist, the important point is not how directly a subjective experience results from the activity of particular cells, but the fact that the cells in question, photoreceptors or striate neurons, have the spectral or pattern-selective property that makes it possible to distinguish redness from other colours or edges from non-edges. The ability to discriminate can be measured, whereas a subjective experience is just perceived.

Let me continue my historical account of how current knowledge of perceptually important neurons has been reached. As Hubel and Wiesel showed, the striate cortex is the first point in the visual pathway where cells can be found that respond to excitation through either eye. Some such cells greatly prefer to receive excitation through both eyes together, and it was natural to ask whether all such cells preferred binocular excitation at one particular disparity, or whether different cells preferred different disparities. Pettigrew, Blakemore and I looked at this question and found cells whose receptive fields lay close together in the visual field, yet required different separations of the targets presented to the two eyes in order to elicit their maximum responses (Barlow, Blakemore and Pettigrew, 1967). These different separations would only occur naturally for objects lying at different distances from the cat, and we therefore felt reasonably certain that the cells were selective for stereoscopic depth. There is still a little doubt as to whether this difference could have been caused by inadvertent relative movement of the two eyes in the interval between the two records, although we thought our controls showed that this was not the case. I do not think the issue has been finally settled in the cat (Ferster, 1981), but the results of Poggio and Fischer (1977) in the monkey support the notion that different cells respond selectively to objects at different distances.

I shall jump to another example of a cell at a much higher level that responds to a perceptually important feature. Figure 4 shows a unit recorded from infero-temporal cortex of macaque by Gross, Rocha-Miranda and Bender (1972). This gave a weak response to many stimuli waved in front of the animal over a considerable region of the visual field, but the strength of the response varied with the characteristics of the stimulus. The numbers under each object indicate the authors'
subjective assessment of the strength or vigour of the response: note how this increases with the resemblance of the target to a monkey's hand, and even the addition of the curvature in the final example made a difference.

An isolated instance worked up in this way is not, perhaps, too convincing, but Perrett, Rolls and Caan (1982) were able to find and consistently record from cells that responded reliably to faces, and one such cell is illustrated in Figures 8 and 9. Of course one already knew that faces are very important socially to monkeys, and the main difficulty is to exclude the possibility that these cells lie in these important response pathways, the recognition and perception of the face being done elsewhere. I don't think one can completely exclude this possibility, but they have done numerous controls in an attempt to do so, and they have done a good job of convincing me that these units really are "face-detectors".

A Model for Perception

I think these results have gone a little way towards filling the gap that I found so painful when listening to Bartlett's introductory course of lectures, namely that one had absolutely no way of conceptualizing what goes on in the brain when one "remembers", "thinks" or "perceives", except by using purely verbal elaborations on those very words. Let me try to formulate more precisely what can fill this gap.

First, I think we now know with reasonable certainty that, whatever the nature of the informational transactions that underlie thought, their currency is that of nerve impulses in nerve cells. When one perceives or thinks, this must be associated with or result from volleys of impulses travelling between nerve cells.

The second conclusion is both less certain and more difficult to express, but I think it takes us towards understanding the unifying, interpretive, aspect of perception. It is that the part that a single active cell plays becomes more important as one ascends in the system. At low levels, many cells take part in the transactions, whereas at high levels each active cell combines information from many lower-level cells; since each active cell unites information from many lower cells, fewer of them need be active. I think this is an inevitable conclusion from the fact that neurons are found which respond to properties of the stimulus such as movement, distance, colour and likeness to a hand or face, which require information to be combined from many early-level neurons.

There is an important anatomical fact linked with this unifying property of higher neurons: there are vastly more neurons available to carry the representation of a body of sensory information, such as a visual image, at the higher levels in the brain than at lower levels. This is shown by the numbers in the histogram of Figure 5: note that the scale is logarithmic and that the number of neurons available to carry the image increases from just over a million in each optic nerve to well over 100 million in the striate cortex.

I have tried to summarize these facts in the scheme shown in Figure 6. Now my brain has cells whose trigger features are diagrams of this sort, and when they fire I am filled with a sense of incredulity and mistrust. Perhaps you distrust them as much as I do, but the idea it
case in the optic nerve. I shall look at the informational balance sheet of a transformation like that suggested here in the next figure, but first look at the analogy suggested in the lower part.

Consider the symbols used in written language. We start with the parts of letters—the dots, strokes and pothooks out of which they are formed. A good alphabet can be formed from only about a dozen such elements, and even a short text contains many samples of each. Next, we have the complete letters; there are nearly 100 of these, including uppercase, numerals and punctuation, and each is used less frequently. Finally, we have complete words, of which there is a vast number, many of which will not occur at all in a short text. I hope you see the analogy; the small number of letter-elements corresponds to the relatively small number of cells carrying the low-level representation, the larger alphabet of the letters themselves corresponds to the larger number of cells at an intermediate level, and the vast number of words corresponds to the vast number of cells available to carry the high-level representation. It is a transformation analogous to that from dots, pothooks and dashes to fully formed words that I think occurs in perception.

Table I shows the informational balance sheet of a transformation such as I have suggested. To illustrate the principle I have assumed that the total information, all derived from the stimulus, is unchanged (see bottom line). This may be thought misleading, for some models of perception attach primary importance to a "filtering" operation that passes important and rejects unimportant features of the sensory messages. Such rejection or loss of information undoubtedly occurs, but I am more impressed by how much is preserved and by the importance of recoding or rearranging the information; because this is the aspect I want to emphasize, I shall try to show the essence of this rearrangement in a model without any information loss. Actually, loss or reduction of information makes the task easier, for a reason that will shortly become apparent.

The result of distributing the information among a larger number of neurons while keeping the total information constant is that the average amount of information each of them must carry is reduced. This can be done by reducing the average frequency with which these neurons fire, so that they are used more redundantly in the sense that the a priori probability of a given cell being active is further from the figure (0.5) that would optimize the information each carries. But because the response of a neuron then becomes a more improbable event, when it responds it conveys more information, whereas in the inactive state it carries very little. In this way the unit of currency—an active cell—is increased in value at the higher level. Notice that if information is lost or
Table I

<table>
<thead>
<tr>
<th>LEVEL</th>
<th>EARLY</th>
<th>MIDDLE</th>
<th>HIGH</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of cells</td>
<td>$10^6$</td>
<td>$10^7.5$</td>
<td>$10^9$</td>
</tr>
<tr>
<td>Av. No. active</td>
<td>$5 \times 10^5$</td>
<td>$10^5$</td>
<td>$6.6 \times 10^4$</td>
</tr>
<tr>
<td>Av. proportion active</td>
<td>0.05</td>
<td>0.003</td>
<td>0.000007</td>
</tr>
<tr>
<td>Av. bits per active cell</td>
<td>1</td>
<td>8.2</td>
<td>14</td>
</tr>
<tr>
<td>Av. bits per inactive cell</td>
<td>1</td>
<td>$4.8 \times 10^{-3}$</td>
<td>$1 \times 10^{-4}$</td>
</tr>
<tr>
<td>Total bits for active cells</td>
<td>$5 \times 10^5$</td>
<td>$8.6 \times 10^5$</td>
<td>$9.2 \times 10^4$</td>
</tr>
<tr>
<td>Total bits for inactive cells</td>
<td>$5 \times 10^5$</td>
<td>$1.4 \times 10^5$</td>
<td>$8 \times 10^4$</td>
</tr>
<tr>
<td>Total for all cells</td>
<td>$10^6$</td>
<td>$10^6$</td>
<td>$10^6$</td>
</tr>
</tbody>
</table>

Note: This shows the informational balance sheet for a transformation such as that of Figure 6. To demonstrate the principle, it is assumed that no information is lost, and the third line shows the result of calculating what proportion of the cells need to be active, on average, in order to carry this unchanged amount of information. The consequence of the reduced a priori probability of being active is that the information conveyed when it is active is greatly increased, as shown in the fourth line, even though the average information conveyed by a high-level cell obviously decreases as the numbers increase.

rejected in these transformations, the frequency of firing of neurons necessary to carry the information would be further reduced; hence the case I have taken, in which there is no loss of information, is actually the hardest.

The important point, shown in the fourth line, is that an individual neuron can, after such a transformation, carry 8 or 14 bits of information. Let me remind you that Shannon’s analysis of written English led him to an average of less than 5 bits per word, so there is a generous margin available if I suggest that the firing of a high-level neuron might correspond to a perceptual event of the sort of complexity and importance that a word has.

It seems to me that forming a representation of an image, or any other large body of information, using a small number of very informative symbols (“cardinal cells” I called them previously—Barlow, 1972) may be a good translation into informational terms of the phrase of Bartlett’s that I recalled earlier and to which he attached such importance in all thought processes—“the effort after meaning.” Of course these valuable symbols will then form, and eventually evoke, all sorts of other associations, but to my mind the difficult step—the one we would dearly love to understand better—is that of forming a representation of sensory messages in which the symbols employed are each highly important and therefore worth forming further associations to.

So far I have argued, first, that something of this sort is suggested by the results of single unit recordings, and, second, that the large number of cells at higher levels makes it possible for a single cell, when active, to convey much information. That is only the supposed end result of the transformation, and in this lecture I cannot possibly face the issue of how it is actually brought about. It is widely recognized that representing a visual scene must be a complex and difficult task which 20 years of effort in artificial intelligence has hardly made a dent in, and there is only time for me to make two points about it. First, it must be a multistage process, and one can be mildly optimistic that computer simulation will shed light on its intricacies (see, for instance, Marr, 1982; Ballard, 1984). Second, exploitation of the redundancy in the input that results from the complex structure of associations it contains must play an important part in the process; perhaps we are beginning to see how the brain might achieve this (see Phillips, Zeki and Barlow, 1984; Barlow, 1985).

Instead of expanding on this, I want to test these ideas against the evidence on the performance of neurons. In order to make as clear as possible what is being tested, I shall propose a specific psychophysical linking hypothesis.

A Hypothesis to Test

The crucial question is: Are single neurons at high levels sensitive, reliable, quick and accurate enough to subserve the representation of important events? Is it, for instance, conceivable that the firing of one neuron would be important enough to trigger a major decision, such as stopping at a traffic light? Of course I am not suggesting that there is just one “red-traffic-light cell” responsible for this decision: if you understand the spirit of the scheme you will realize that it proposes a large
number of such cells in parallel, any one of which might trigger the
decision. But I am suggesting that one would be enough, and the
following psychophysical linking hypothesis expresses this claim:

Whenever two stimuli can be distinguished, in normal life or in a
psychophysical experiment, then proper analysis of the impulses occur-
rning in a single neuron would enable them to be distinguished with equal or
greater reliability.

One can argue for the correctness of this hypothesis along the
following lines. Nerve cells are the only means we know about whereby
items of information occurring in different parts of the brain can be
combined; sensory discriminations require the combination of infor-
mation from different parts of the brain; therefore this operation must
be performed by a cell, and if one could record from the cell that did this,
one would obtain results at least as good as those of the whole animal. Of
course two or more cells may each combine enough information to
enable the task to be done, and no doubt this is the commonest
occurrence both in real life and under the conditions of a test; but I don’t
think more than one is necessary because, if it were, I don’t see how the
information from the two or more essential cells could be combined,
except by another cell; and then that cell would be the one to which the
principle applied. Thus the challenge is: Can it be proved that one
neuron is not enough?

Because of the difficulty of finding the appropriate neuron, such
disproof of the hypothesis is likely to be difficult, but the history of
attempts to measure the performance of single neurons encourages me to
think that the hypothesis holds, and I want to show some evidence
supporting this.

**Some Quantitative Questions**

Early measurements of the sensitivity of retinal ganglion cells showed
appallingly high thresholds superimposed on a very noisy maintained
discharge, and it used to be held that the high sensitivity achieved at
absolute threshold would only be possible by averaging the responses
from many fibres. Measurements I made on the cat (Barlow, FitzHugh
and Kuffler, 1957) cast doubt on this conclusion, and I believe later ones
(Barlow, Levick and Yoon, 1971) confirm that it is untrue. It can be
shown that some ganglion cells give reliable responses to only 15 quanta
(on average) at the cornea, so such a cell could mediate the detection of a
flash of this intensity, which is probably rather below the behavioural
absolute threshold for a cat. It is important to realize that any particular
cell would only be responsible when the stimulus fell in exactly the right
place. Also the intact cat has the problem of discounting false positive
responses from all the cells in regions where the threshold stimulus
might be: thus the issue is not completely settled by this result, but on
the other hand it certainly weakens the attacks of opponents of the
linking hypothesis.

What about cortical neurons? Here again early results suggested gross
insensitivity and unreliability, but with improved methods better results
have been obtained. Tolhurst, Movshon and Dean (1983) took the
approach of comparing the reliability of psychophysical responses
obtained from psychometric functions. To estimate the reliability of a
cell’s response they plotted the proportion of occasions on which a
certain criterion number of impulses was equalled or exceeded. These
“frequency-of-spiking” curves are flatter than psychophysical “fre-
quency-of-seeing” curves, indicating that the neural responses showed
more variability than a typical subject, but they concluded that the
reliability shown in a psychophysical test could be achieved by utilizing
the responses of as few as four cortical neurons. It may be important that
the preparations they used were anaesthetized, which would not have
been conducive to the cortical neurons’ reliability.

These results have been improved upon by Parker and Hawken
(1985), who measured the contrast sensitivity of cortical neurons in
monkeys and compared this with that of humans viewing identical
targets, which were portions of spatial sinusoids. In many cases they
found that the single neurons had greater contrast sensitivity than the
humans. Again there is the problem that the human subject has to allow
for the possibility of false positive responses from the many other
cortical neurons that might have responded to a stimulus in the
conditions of the test, but in other respects the single cell was doing as
required by the hypothesis.

Acuity also used to be a problem, but Figure 7 shows that some
cortical neurons are well able to respond to gratings up to the limit
expected from psychophysical performance.

Many problems remain to be examined quantitatively, but this short
survey does not suggest that single cells are as incompetent as they
initially seemed; I shall use a final example from a higher level. The early
recordings from “face detectors” suggested that they responded to
almost any face, and this seems to be true for some of them. But later
experiments (Perrett, Smith, Potter, Mistlin, Head, Milner and Jeeves,
1985) showed that other cells distinguished reliably between the faces of
two humans whom the monkey knew, and they continued to do so
despite a number of potentially disrupting manoeuvres. This exper-
iment is shown in Figures 8 and 9.
Figure 7. A. The contrast–response curve of a complex cell from lamina IVg of striate cortex of vervet monkey, which responds at substantially above its maintained discharge rate (point at lower left) to a grating of almost 60 cycles/degree.

B. Probability of at least one spike in the response to a 1-sec exposure of a drifting grating of contrast 0.7, calculated from the 20 presentations used for A above. A detection rate of 50% correct would have been obtained for a 55-cycle/degree grating, with 5% false alarm rate. This result suggests that a single cell can subserve discrimination at the resolution limit, as the proposed linking hypothesis requires (from Parker and Hawker, 1985).
I do not know if the more exciting of these two faces corresponded to a red or a green traffic light, but it does seem to me that this cell makes a discrimination as difficult and important as the one I initially gave as an example. Of course one must bear in mind that there are presumably many cells capable of making the same discrimination under different circumstances, so it would be naive to identify this single cell as the one and only mediator of the perception of PS's face. It is also true that we do not know the means by which such a cell is able to make the discrimination. Nonetheless I think one can conclude that the response of a single cell is sufficient for a major decision, and that the psychophysical linking hypothesis I proposed is not disproved and quite likely to be true.

Back to Psychology

We now know the sort of thing single neurons can do: How might these abilities be organized to enable the brain to perceive? I think this has now become the main question facing perceptual psychology. It seems to me that recent work on the cortex has opened up some opportunities that should not be missed, but although much of this work is described in psychology texts, it has not been related successfully to psychological knowledge of perception. Briefly, Talbot and Marshall (1941), Daniel and Whitteridge (1961), and Hubel and Wiesel (1974) have shown that there is a very precise map of the visual field in the primary visual cortex; this contains pattern-selective neurons that pass on the information to a host of secondary visual areas with much less precise topographical maps (reviewed by van Essen, 1979). There has been some argument, but it now seems likely that the idea proposed by Zeki (1978) is correct: these other areas specialize in particular aspects of the image, such as motion or colour. Now this new knowledge of the anatomy and physiology of the brain is profoundly unsatisfactory if it does not start to answer the basic question: "How does visual cortex enable you to see? How does it tell you about your environment?" Those are questions the psychology of perception ought to give some ideas about, and I think it does.

For the visual system, Bartlett's phrase "the effort after meaning" implies that it must find out about objects in the visual field, for it is objects that have meaning for us. I think the first hint of what is needed to do this came from the work of Guzman (1968) at MIT. He was writing a computer program that could solve the problem of labelling the blocks in a line drawing of a jumbled heap of them, and he found it necessary to use what he called "linking features" or "linking characteristics" when searching through the store of information in the com-
puter's memory to find all the parts of a single block. In this example, the linking feature that was required to organize the search was the orientation and collinearity of edges: two collinear lines were likely to belong to the same block, even if they were widely separated in the image. In much the same way, when trying to solve a jig-saw puzzle one looks for "blue sky" or "brickwork" or "foliage" in order to narrow the search for matching pieces. For me, at least, this work of Guzman's gave the first hint of the functional importance of the factors that the Gestalt psychologists had shown to produce segregation of figure from ground: they are the factors that reduce the search time in finding which parts of an image belong to the same object and hence belong together. More recently, the work of Marr (1982) and his colleagues has told us more about how visual scenes can be analysed, though interestingly enough much of this work has been devoted to parts of the process that must occur at an earlier level and therefore precede those with which Guzman was concerned.

The task performed by the visual system is long and complex. Elsewhere we have argued (Phillips, Zeki and Barlow, 1984) that the most important aspect of this task is the detection of the statistical regularity, or order, that results from objects, and Table II shows the logic of this operation. Perhaps it begins to make sense of the organization that has been found in the visual pathways. The first step is to find the local characteristics of the image that are likely to be shared by the whole of an object. These local image characteristics seem to correspond to the features that cause segregation of figure from ground in Gestalt terminology, and there is surprisingly good agreement between the list of characteristics that cause figure-ground segregation and the pattern-selective characteristics of neurons in the primary visual cortex (Barlow, 1981).

Most of these facts have been known for a number of years, so it is reasonable to ask: Why has not figure-ground segregation been tested in animals with primary visual cortex ablated? Why has this not been tested in animals with localized lesions in those parasagittal areas that Zeki and I think specialize in each of these linking, or segregating, features? The answer must be that psychologists have not yet incorporated these physiological and anatomical results into their thinking, and that psychologists themselves have been too busy with their own immediate physiological and anatomical problems to appreciate the relevance of their results to the psychology of perception. I suspect that there are many similar opportunities waiting for those who want to understand the physiological basis of psychological processes and the psychological rationale for physiological mechanisms.
### Table II

<table>
<thead>
<tr>
<th>Objects:</th>
<th>Therefore:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tend to be localised in space</td>
<td>Preserve topology of the image</td>
</tr>
<tr>
<td>Tend to have same depth and motion in all their parts</td>
<td>Detect local depth and motion in the image</td>
</tr>
<tr>
<td>Tend to have similar surface characteristics throughout their extent</td>
<td>Detect local colour and texture in the image</td>
</tr>
<tr>
<td>Tend to extend beyond patch accessible to one neuron</td>
<td>Map according to linking characteristics, not only image topology</td>
</tr>
<tr>
<td>But none of above are fully reliable</td>
<td>Therefore weight information according to its reliability</td>
</tr>
</tbody>
</table>

Note: This shows the logic of object recognition. It is suggested that the first three steps in the right-hand column are achieved in striate cortex, the fourth in the parastriate areas. Since none of the cues are infallible it is necessary to combine, and weight appropriately, information coming from different sources of variable and unpredictable reliability; hence the need for each source to signal its own reliability.

### Conclusions

There are two conclusions I would like you to take away from this lecture:

The first is that we do now have a conceptual model of how the brain works; it lacks detail, but it is a model that has room in it for psychological concepts such as those of the Gestalt school, or Bartlett’s “effort after meaning”.

The second is that the model needs to be developed and tested by asking psychological questions and attempting to answer them using physiological techniques.

In other words, I think the advice Bartlett gave me 40 years ago was correct, but now the subject has advanced to the point where it is crucially important either for the physiologist to know the appropriate psychological questions to ask, or for the psychologist himself to undertake the physiology.

### REFERENCES


