

THE PAST, PRESENT AND FUTURE OF FEATURE DETECTORS

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If one knows where ideas have come from and how a subject has developed one gets a much clearer view of which direction you are pointing and what the next problems may be. I shall therefore start by looking at the past history of feature detectors, then I shall talk a bit about my present work, and I shall conclude with a brief guess at the future.

Past history of feature detectors

The idea of feature detectors arose in the early fifties and I think the prime reason was a discontent with the two ideas about the physiology of the sensory pathways that were dominant at that time. The first idea was that of projection maps, which arose from the work of Adrian, Bard, Marshall, Woolsey and others (Adrian, 1947; Marshall, Woolsey and Bard, 1941; see also Fulton, 1949). It was shown that a sensory surface such as the skin, the retina, or the cochlea, was simply mapped topographically onto the cortex. The discovery was important, but physiologists were rather inclined to leave it at that point and say "Well, now we've got the map up into the brain it is for the psychologists to find out what goes on there." However if you thought about it at all, it was unsatisfactory to suppose that the only thing of physiological interest that happened in the retina or in those complicated nerve cells and synapses in the lateral geniculate was simply to map the visual image on the cortex; that would really be rather a disappointing conclusion, for one might well hope to be able to find out more about the kind of operation that goes on high in the nervous system by studying transformations of sensory messages early in sensory pathways.

That was the first idea that seemed inadequate, and the second one was the concept of a receptive field as it had been left by Hartline (1938; 1940a; 1940b). He was the first person to map receptive fields in the retina; this was another important advance, but the aspect of

it which was disconcerting was the enormous size of the receptive fields and the supposition that they simply responded to the summed light within their area. Hartline worked on a variety of animals, but much was done on the frog, which one knows is a very visual animal capable of a high grade of visual performance, and yet the fields which he mapped were absolutely enormous, covering ten or twenty degrees in visual space. When I started working on the frog's retina I remember explaining, actually to Alan Hodgkin, what I was trying to do; I said that I didn't see how frogs could possibly read and write if they had summing receptive fields that size, and his answer was, naturally enough, that they don't read and write. But they do catch insects and they depend on their eyes for their living, so I felt their eyes were bound to have good resolution.

Those were the reasons for being worried about the physiologists' description of what went on in the visual pathway, but there was a positive stimulus for thinking in a different direction, and this came from the ethologists. About that time Tinbergen (1951) and Lorenz (1952) were putting forth the idea of specific releasers for particular pieces of behaviour in animals. We were hearing of examples like the red dot on the herring gull's beak toward which the young make their pecking movements, and the various releasers of the different items of behaviour in the stickleback. Now physiologists of the central nervous system were not at that time thinking atomically; they were frightened at the prospect of trying to explain a complex piece of behaviour of the whole animal in terms of what single cells do, and nobody would have dreamed of trying to do it. But the idea of accounting for little items of behaviour in terms of single cells specifically tuned to red dots and things like that was quite a different matter that did seem to be a possibility.

This possibility should have been evident when I started looking at the frog's retina but I actually had a simpler idea in mind. If you measure the psychophysical threshold of a test stimulus as a function of its size, when it's very small it follows Ricco's law: that is, the threshold is inversely proportional to the area and it is as if it was summing all the light within a particular region. But when you get to larger areas it obeys Piper's law, which says that the threshold is proportional to the square root of the area; alternatively you can say that threshold is inversely proportional to length of the edge. So was it possible that the units which had these enormous receptive fields were not simply summing light all over that large area, but were

abstracting the edge and responding in proportion to that? Were they "edge-detectors", not just transducers of total light energy?

To test this I did the experiment on a frog retinal ganglion cell shown in Fig. 1 (Barlow, 1953). The log of the radius of the spot is plotted horizontally, and $\log(1/\text{threshold})$ vertically.

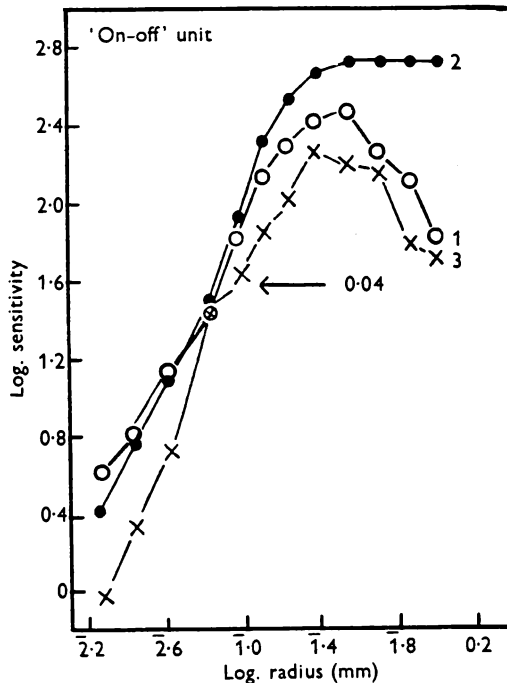


Figure 1: Test for "edge-detectors" by measuring the threshold of an "on-off" ganglion cell of the frog's retina to spots of varied radius. Curve 2 was calculated from a map of the whole receptive field on the basis of summation of sensitivities of the parts covered by the spot. Curves 1 and 3 were experimental measurements of threshold done before and after the mapping. If the unit had done simple summing the points would have followed curve 2; if it had done "edge-detecting" they would have risen with unit slope on these coordinates. They do not fit either hypothesis well, but their decline at large radius revealed the presence of the inhibitory surround (from Barlow, 1953).

I was hoping that the points would follow a line of slope 1, indicating that threshold was inversely proportional to the length of the edge. The line numbered 2 was the alternative prediction, that sensitivity was simply the sum of the sensitivities of the retinal regions covered by the spot. Well, however hard I looked I could not

make that into a line of slope 1, so I was a bit distressed, but I got some comfort from the decline in experimental points at large radii, because if they were edge-detectors one would expect sensitivity to decline when the edge of the spot fell outside the receptive field. And then it occurred to me that there was a very much simpler explanation of these things; it might be simply that there was an inhibitory effect from the surround, and indeed there was, as Fig. 2 shows. If you put the spot in the centre you get a good response at both "on" and "off." But if you turn the other spot on and off at the same time you get very much less. The original idea about edge detection by means of some mysterious process that abstracted the edge turns out to be wrong, but on the other hand, something very similar is achieved, though on a coarser scale of distance, by having the inhibitory surround.

For me, this evidence for lateral inhibition was the beginning of the idea of feature detection, and it developed further in the direction of the lead given by Lorenz and Tinbergen. If you really want to stimulate these cells vigorously you will find yourself delivering a type of stimulus to the receptive field which is similar to the stimulus that activates the frog into violent feeding behaviour in real life. I remember on one occasion qualitatively testing various spot sizes and rates of movement and flicker to see what drove a cell best, then doing sums for getting the same angular subtense of a stimulus in the real world of a frog, and finally taking a piece of paper mounted on a wire down to the frog-tank in the basement. The effect was dramatic: the tank was transformed from a torpid mass of lifeless bodies into a cage of active, prey-seeking beasts. So the idea of explaining the innate releasers of Lorenz and Tinbergen in terms of the functions of single nerve cells did not seem impossible, and the surprising thing was that a substantial part of the lock-and-key mechanism appeared likely to reside in the retina. Of course one now knows from the work of Ingle (1968) and others that it was too naive to suppose that a single class of retinal ganglion cell was the only thing that determined feeding behaviour, but nonetheless the retina contains selective filters for fly-like objects.

This work received publicity from a surprising source, the U.S. Navy; William Neff was ONR representative in London and circulated an account of a lecture I gave in 1952 on "The Psychology of the Frog's Retina" to US Vision labs. And there were others talking about similar things, such as Waterman, Wiersma and Bush (1963, 1964) with their

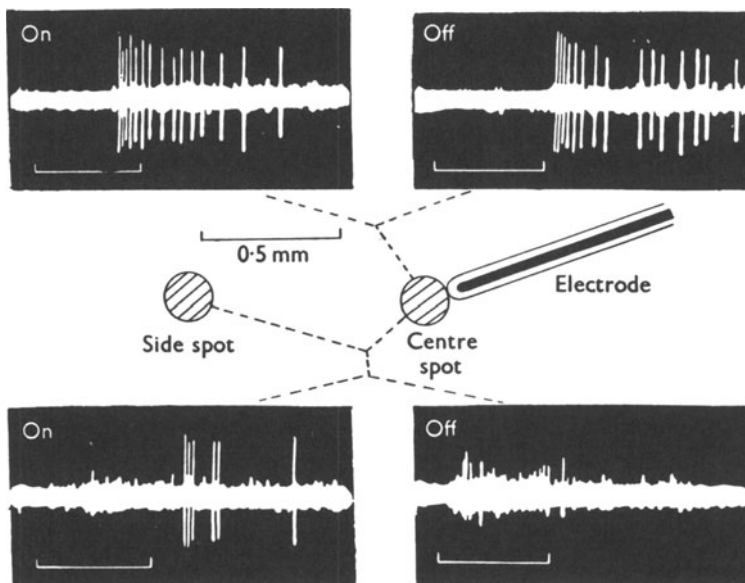


Figure 2: Lateral inhibition in the frog's retina. One spot of light was placed near the centre of the receptive field of a ganglion cell; this gave vigorous bursts at "on" and "off", as shown in the records at top. A second spot was placed almost 1 mm away, and this inhibited the response from the first spot when turned on and off synchronously with it, as shown in the lower records. This shows the presence of a silent inhibitory or suppressive surround; unlike in the cat, the second spot gives no response at either on or off by itself (not illustrated). Time calibration is 200 msec. (From Barlow, 1953).

work on crustaceans. But I don't think Feature Detectors really caught on until 1959, when Lettvin, Maturana, McCulloch and Pitts (1959) published their famous paper on the frog retina, and when Hubel and Wiesel (1959, 1962) started publishing their work on the cat cortex.

It is an interesting question how much any of us were actually looking for what we found. One person whose name I haven't mentioned yet, who certainly was selling the idea of feature detectors very prominently around that time was Oliver Selfridge (1959) with his "Pandemonium" model. This is really a set of feature detectors arranged in a particular way, and of course the "Perceptron" of Rosenblatt (1959) was also a serial hierarchy of feature detectors.

Hubel and Wiesel always denied strenuously that they were looking for anything; they just found out what was actually there, and this was a very good line to take, especially as the rest of us could not help looking for what we hoped to be there. I am not certain this story of Hubel and Wiesel's discovery is true; it is said they were intent on mapping out the receptive fields in the cortex using little spots or light, or black dots, and for this they borrowed from Steve Kuffler a set of black dots on glass slides that we had used down in Johns Hopkins. But in the journey from Johns Hopkins up to Boston they had been cracked, so that the slides had lines on them as well as the dots, and they observed that a line of the right orientation was a much better stimulus for their cortical neurones than any black dot. If true, that should be empirical enough for anybody, and I think it should bring home the fact that you need the concept of feature detectors to describe the way neurones in sensory pathways behave. Orientational selectivity cannot be an uninteresting artefact.

Before leaving the past let me illustrate two other types of feature detector with which I have been involved. Fig. 3 shows a directionally selective cell of the type Levick, Hill and I found in the rabbit's retina (Barlow, Hill and Levick, 1964); Maturana and Frenk (1963) described similar units in the pigeon retina. First, if you map out the receptive field with a stationary spot there is nothing to tell you of its most interesting property; everywhere inside the O's just gives a brief burst at both "on" and "off." But when you test with a moving stimulus you get really dramatically asymmetric responses. For the spot moving in one direction you get hardly any, just two, impulses. But when you move it in the opposite direction you get a vigorous, sustained, burst containing, in this case, 79 impulses. In other directions you get intermediate numbers. Incidentally, we came across this really striking property of cells entirely by accident; we were not expecting it or looking for it at all.

The other type of selectivity I want to illustrate is for disparity in cells of the cat cortex. Figure 4 (from Barlow, Blakemore and Pettigrew, 1967) shows two units, one on the left and one on the right. You have to imagine the cat looking at the plotting screen with its eyes slightly diverged, so that for the left unit, to stimulate the left eye you have to put the object as shown at the top and to stimulate the right eye it has to be as shown in the second row. So you measure the separation of those two stimuli and move them together

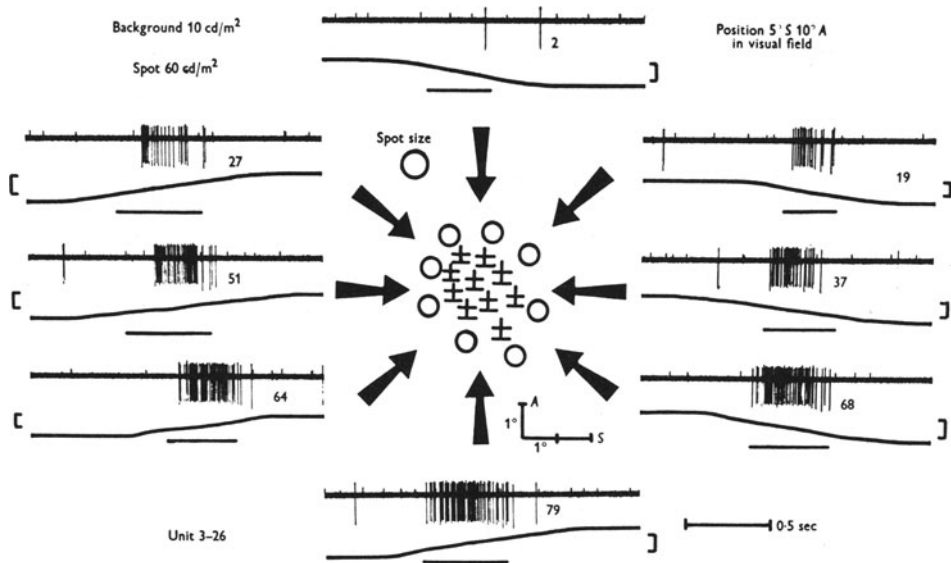


Figure 3: Directional selectivity in a retinal ganglion cell of a rabbit. The receptive field was mapped with a stationary spot and gave responses at "on" and "off" at all points within the O's, and no responses outside. When tested with a moving spot it gave a vigorous burst of 79 impulses for anterior movement (upward in the figure), but only 2 for posterior movement. Other directions gave intermediate values. The slanting line below the trace of impulses monitors the movement of the spot, the calibration marks indicating 5 degrees in the visual field. Other units respond selectively to posterior, upward, or downward movement. (From Barlow, Hill and Levick, 1964).

and then you get a big response, 17 impulses on this trial, much bigger than the sum of the two eyes separately. If you do it at the wrong separation you get fewer, less even than with either eye alone. The point to notice is that for the optimum response, the stimuli have to be more than 6 degrees apart on the plotting board; that is not a true disparity of 6 degrees, but the sum of the disparity and divergence. The unit to the right is rather similar, but for optimum response the stimuli need to be just over 3 degrees apart. So these two units will respond to objects at different distances and are examples of disparity selectivity.

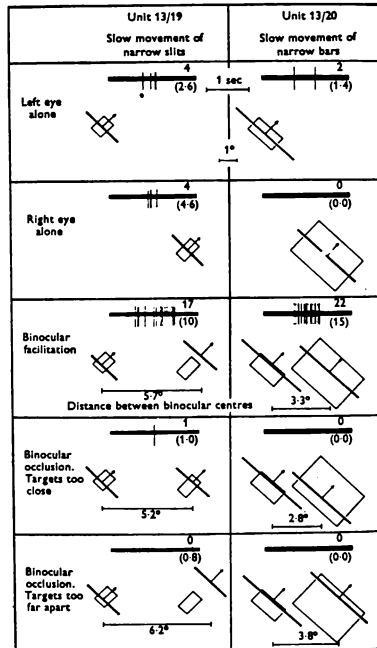


Figure 4: Disparity selectivity in cortex of cat. Two units are shown, one of which showed binocular facilitation when the moving targets for left and right eyes were separated by a distance corresponding to 5.7 degrees on the plotting screen, the other when separated by 3.3 degrees. The eyes are slightly diverged in the paralyzed preparation, but if converged by an amount appropriate for the first unit to respond optimally to a real object, then an object capable of stimulating the second unit would have required 2.4 degrees additional convergent disparity, and would therefore have had to be much closer. The number above each record shows the number of impulses in that trace and the number below in parentheses gives the average in 5 repetitions. Notice that there is no overlap in the range of disparities for which the two units respond. (From Barlow, Blakemore and Pettigrew, 1967).

In this case Pettigrew, Blakemore and I deliberately searched for disparity selectivity; we thought it would be there and it was. But even though theoretical reasons for expecting feature selectivity have been advanced, the overwhelming fact is that you need the concept of feature-selective detectors just to describe the findings when recording from neurones in sensory pathways. Whatever their future, our knowledge of feature-detectors represents a substantial addition to our previous knowledge of topographical mapping and of non-pattern-selective receptive fields.

Feature detectors in human psychophysics

Most people would accept the proposition that, if frogs, cats, rabbits and monkeys have feature detectors in their visual systems, so do humans. But how do we obtain evidence for their operation in human sensation and perception? There are a host of problems in relating neurophysiology and sensation. For instance it can be said that neurophysiology gives us details of the hardware, whereas psychophysics only tells us about overall performance, which can be achieved by many different types of hardware; or that neurophysiology describes local operations performed on the image whereas the most important aspects of sensation are global; some people might even go so far as to say that the psychological approach can tell us nothing about mechanism, though I think that is falsified by the successes of psychophysics in elucidating the mechanisms of colour vision, and the limits of sensitivity and resolution. I do not claim to have overcome these very big problems, but it is my belief that they can be overcome if one approaches the problem the right way, and I think the right way has been shown to us by the successes I have just mentioned. So my objective in the work that I shall now describe was to make measurements of perceptual performance of a type that must tell one something, at least, about the necessary hardware, and I have picked a problem that certainly involves global, not purely local, operations. I hope it will become clear where feature detectors come in later.

There are two key ideas in this approach. The first is to use a measure of performance that will allow comparisons to be made at quite different tasks. There is no problem if the task is always very similar. Suppose, for instance, that one believes the visual system has "bar detectors" for vertical and horizontal bars, but not for obliques, which is probably the case in rabbit retina (Levick, 1967); if this was the case in humans, one should be able to get evidence for it by measuring a subject's contrast sensitivity for bars at different orientations; it should be poor for obliques. But it would be different if one was varying the length or width of the bars, or comparing bar-detecting with movement or disparity detection, because changing the task in these ways would make it physically more difficult or easier. How then is one to compare performance at totally different tasks? The only answer I know is to measure each performance

by comparison with an ideal instrument for performing that task. By making use of concepts derived from statistical decision theory and information engineering this can be done for a good many perceptual tasks, and it yields a figure for efficiency; it answers the question "What fraction of the information available for performing this task did the subject actually use?" Naturally we expect, using this efficiency measure, to find that subjects are better at some tasks than others.

The second key idea of this approach is to search for tasks that human subjects can be shown to perform efficiently, using these absolute measures. Now loss of efficiency is irreversible; if information is not collected, or is thrown away, no kind of central processing can make good this loss. So if a subject performs efficiently his physiological mechanisms must be preserving the requisite information, and the hope is that one can find tasks that optimally match his physiological mechanisms, thereby defining their most important functional property.

Notice that the efficiency measure can, in principle be used on a neurophysiological preparation; in the future years we may be able to say "Human subjects detect bars with X% efficiency; we find single neurones in monkey visual cortex that perform with equal efficiency, and we therefore believe that human subjects detect bars by using such feature detectors in their own brain". Strictly, we should say "we therefore see no reason for disbelieving", but the message is the same.

An important characteristic of this approach is the assertion that there is a limit to how well a perceptual task can be performed. A lot of psychophysical measures, such as those involved in acuity and colour matching, relate to the physical aspects of the stimulus; you try and explain how well you do them in terms of the quality of the retinal image or in terms of the photo-sensitivity of the pigments and so on. In the type of problem I am going to deal with here we are not concerned with physical limits of that sort, so the first thing to decide is what else might limit the performance of feature detectors, and the overall performance of the whole animal, when making a higher level perceptual decision.

I shall argue that in many cases, perceptions are limited by noise and not by insensitivity of the central apparatus. I think most people

are familiar with the fact that if you have an instrumental system designed to measure some particular quantity, it may fail to detect an input for either of two reasons. It may be too insensitive, because it does not have enough amplification, or because the pointer of the output galvanometer has too strong a return spring so that it is jammed up against its stop, or something like that. On the other hand, the limit may be of a different kind if, even in the absence of the stimulus that it's designed to detect, the output pointer or indicator is showing signs of continuous activity. In that case the performance of the system will be limited by signal-to-noise considerations. And I'm going to advance some arguments that that is in general the case with perception.

Most people start with a prejudice in the other direction because of one's subjective impressions. When one looks at an array of photographs, for example, and picks out the face of somebody one knows, one doesn't have the impression of a whole lot of false recognitions going on in one's mind, then the correct one being selected, with some doubt, from a number of false ones. The process seems more like the pointer on a meter coming up to a definitive reading. And likewise with almost all sensations, when you look at them superficially they seem to have this character of being rather certain judgements without an element of background uncertainty. However, that's not the case when you start looking in more detail. For example at the absolute threshold, if you start encouraging people to respond without being quite so certain, you can drive their criterion so far down that they will make almost any desired proportion of incorrect identifications (Sakitt, 1972). The initial impression that perceptions are not perturbed by noise does not stand up to closer examination. That's the first argument.

The second one is rather general and difficult to make convincing. It is simply that one's got to perform some complicated operation on an input which has spontaneous activity; the sensory nerve fibers are not quiet, they're buzzing away like mad most of the time. And it is very difficult to imagine any operation that could be performed on that input that wouldn't occasionally give a false response. There must be false identifications of features, because one could not design a mechanism which would be entirely free from errors.

And the third point is a demonstration. Figure 5a shows the same set of words, but each has been carbon-copied an increasing number of

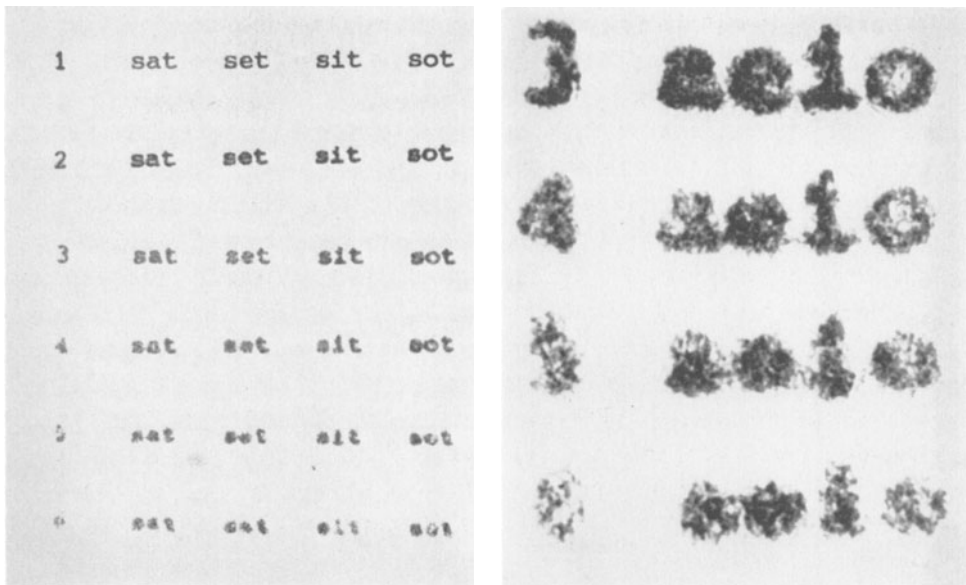


Figure 5: To the left (A) are shown the first to the sixth carbon copies of the same set of words; after the third they become hard to identify. It might be thought that enlargement would improve matters, but the enlargements of the central vowels at the right (B) show that this is not the case. It is the noise introduced in the copying process that impairs perception, and in such cases enlargement, amplification, or contrast enhancement do not improve performance.

times. The fifth or sixth copy becomes virtually impossible to identify. If they were small, you might think that it was merely an amplification problem; if the size could be increased a bit it would be possible to identify them. But that is not so. At the right (figure 5b) are the same letters enlarged and as you see it is obviously not a problem of magnification, but of the background noise in the system. It is plausible to suppose that many other recognition and identification problems are also limited by noise and not by insensitivity.

Now in order to be quantitative about this one must look at the question how well discriminations of signal from noise are performed; it is a statistical task. I wanted to look into a type of perception

which was more complicated and must involve higher level processes than ones involving resolution, sensitivity, or colour. The task I chose is shown in Fig. 6.

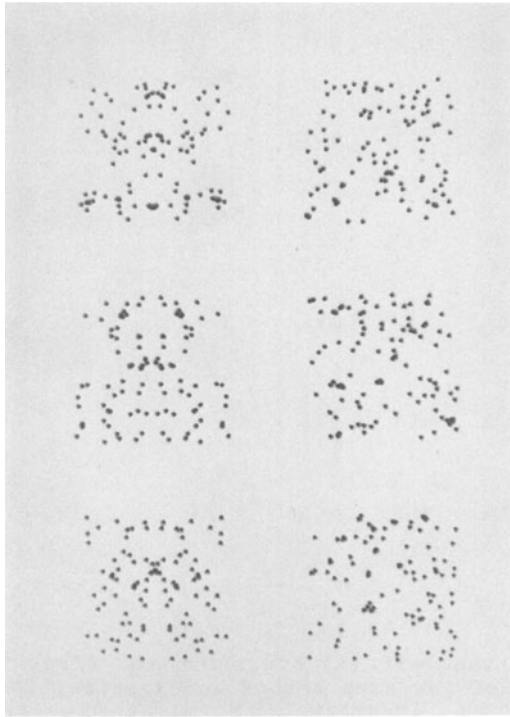


Figure 6: Pairs of computer-generated dot patterns that were either symmetric (left) or without symmetry (right). The subject's task was to assign an example to one population or the other. In these examples he would make no errors, but the limits of the symmetry-detecting mechanism can be explored by making the task more difficult.

These are photographs of the graphics screen of a computer. The three on the left are all symmetric about the mid-line. The three on the right are not. One can feel absolutely certain there is not any simple optical or photochemical explanation for how this is done; you are quite out of the realm of things which are limited by the physics of the eye.

It is clearly more complicated than many simple detection processes in another way because it demands an associative process. If half of a picture is covered you couldn't possibly tell if it was symmetric or non-symmetric. So there must be some way of detecting an association between corresponding positions.

And thirdly, I recalled the days when I tried to persuade psychologists in Cambridge that it was meaningful to talk about the psychology of the frog's retina. They used to come back and say, "Well, that's all very interesting but it's not real psychology at that level; that's ethology or mere physiology; you've got to show how the interesting problems like those of Gestalt Perception are performed before you're really saying anything of the least importance to us". I thought symmetry would be an interesting problem to look at for this reason too. We may not find the mechanism by doing psychophysical tests, but we can at least define how well it works and under what conditions.

The method was as follows. The subject sat in front of a computer graphics screen and for a familiarization period, which could actually be as long as he liked, he simply pressed "zero" or "one" to get either a sample of one of the right hand patterns or one of the left hand patterns of Fig. 6. As you can see, if you did that with those patterns, it would not take you long to realize that when you press the one you always get symmetric pattern. The subject is given every opportunity to learn and verbal instruction was included if necessary. Then the computer gives him a hundred unknowns and it is the subject's job to classify them. If it had been a task like that of Fig. 6, he would have had no problems; he would have got 100% right, but there are ways of making it more difficult and finding out the conditions where the symmetry detecting mechanism breaks down.

These experiments were done with Barnie Reeves, who is now in Oxford, and have recently been published (Barlow and Reeves, 1979). The first thing we did was to find out more about the elementary properties of symmetry detection. From the literature we were not clear whether the axis of symmetry had to be central and vertical. Well, the answer is that it doesn't matter, though one performs best with the axis central and vertical. I should mention that in these experiments the picture was only flashed on for about 200 msec, so the person could not tilt his head or anything like that, and in most cases could only use one fixation pause. It is of course important that you can do this kind of task in a brief flash with no particular difficulty.

We also did experiments in which there was a fixation point on the screen, and the picture appeared either centred, or to the left, or to the right. The subject had no way of anticipating which place it would

occur and could not move his fixation in anticipation. The result was that performance on the centred ones was higher than on the displaced ones. So it is true that you do it better with the axis on the vertical mid-line, but you can still do it when the patterns are displaced up to three degrees into the periphery. These patterns were two degrees across, so no part was falling in the centre of the field of vision, and yet the performance, though it was decreased compared to the centred one, was still quite good.

Obviously the physiological mechanism required to detect symmetry about any orientation and any position in the visual field is vastly more complicated than that required if it had turned out that one could only do it with the axis vertical and in the mid-line. For the latter operation one stereotyped mechanism might be enough, but we now know the mechanism can perform quite a versatile task.

To achieve the aims I set out above we must now try to express in absolute terms how well this task can be done. To do this we must compare the human performance with the best possible performance, and it is only then that we may get evidence that the task is being done so well that we might tentatively conclude that there is a specific mechanism, a "feature detector" for detecting symmetry. How are we going to decide what limits the detection of symmetry and how closely our subjects approach this limit?

These dot patterns were made with a computer, so we know exactly how they were made and it is feasible to say how you should set about testing whether a pattern is from the symmetric set or not. It would actually be dead simple: you take any dot, calculate the coordinates for the mirror dot and look through the list to see if any of them coincides with that. And if you found one mirror dot you could say, "Well that couldn't arise by chance, therefore the pattern must be from a symmetric set". It could hardly arise there by chance because these dots are placed with high accuracy, 10 bits for each dimension approximately, so there are one million possible positions for a dot, and the chance of one of the 100 dots occurring at a prespecified position is very small, unless it has been deliberately put there. As soon as one gets evidence of even a single symmetric pair one can say with reasonable certainty that the pattern is from a symmetric set. However the situation would be very different if the dots were placed with lower accuracy, for then pairs could arise by chance in asymmetric patterns. Notice, moreover, that if the visual system is

not capable of using all the accuracy in the display, then our equipment would be better than the subject needs, and the above argument would also have given a false impression of how easy the task is. Therefore what we did was to decrease the accuracy

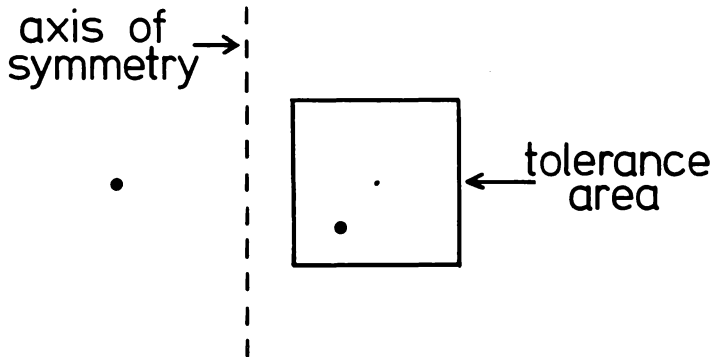


Figure 7: Generating smeared or imperfect symmetry. The position of the dot at left was first selected by the computer; then instead of placing the paired dot at the exactly symmetric position, it was placed at a randomly selected position in a tolerance area. The size of the tolerance area could be varied in order to find how performance at detecting symmetry was affected. (From Barlow and Reeves, 1979).

with which the dots were mirrored. Instead of placing a dot at the exactly symmetric position we placed it in a tolerance area as shown in Fig. 7. Then we varied the tolerance area, the aim being to match the properties of the generating system to that of the detecting system.

Figure 8 gives an impression of what this "smeared" symmetry looks like. It looks as though the symmetric pattern had been dropped on the floor and slightly damaged. The usual task was not to distinguish smeared symmetry from perfect symmetry, but from a completely random

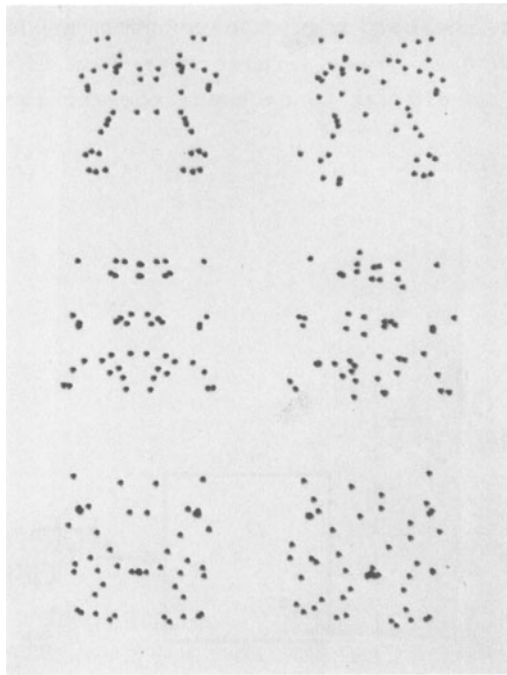


Figure 8: Three examples of exactly symmetric patterns (left), and the same patterns in which the symmetry has been "smeared" (right) by the method shown in Figure 7.

pattern. Figure 9 shows how d' varied at different tolerance ranges. The surprising thing is that you can tolerate a large amount of smearing, of inaccurate pairing, and still perform quite well. The tolerance box in Fig. 7 can be 10 minutes in each direction, and it has hardly any effect on the performance. You should compare that figure of 10 minutes with two-point resolution of one minute, or the accuracy of vernier alignment, which is also a judgement of position, of the order of 10 seconds of arc. The inaccuracy which you can tolerate and still detect symmetry is very large indeed. Symmetry detection does not need a high resolution system.

Now you remember I said just before that if the dots were inaccurately placed one would have problems in the ideal method. Suppose for example that we use 10% accuracy of placing the dot, then you have got only 100 meaningfully different positions to put a dot, and then when you put down 100 at random, some of them will undoubtedly appear in a range which qualifies as being that of a pair.

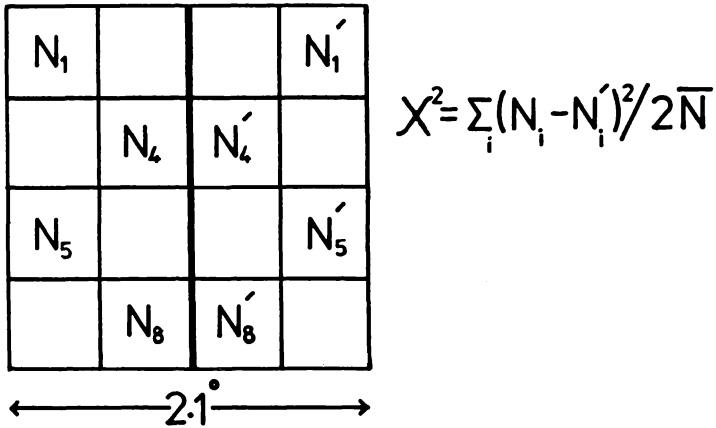


Figure 9: The subject makes errors in detecting "smeared" symmetry, and it is possible to calculate d' for discriminating between the two populations of computer-generated patterns. The experimental values, d_E , are shown here for two subjects and a range of different tolerance ranges. The continuous line shows results of basing discriminations on counts of the number of pairs that would qualify as being placed according to the procedure of Fig. 7, since this is the best possible performance; the scale for this line is at right, and is double the left scale. For tolerance ranges above 10 minutes the curve fits the points; hence $d_E/d_I = 0.5$, and statistical efficiency is 25% (see text, and Barlow and Reeves, 1979).

So how can you tell which patterns come from the paired set and which come from the completely random set? The best way of doing it would be to go through all the pairs--4.950 for 100 dots--and count those which could have been placed as pairs, thus obtaining the total number of such qualifying pairs. In the symmetric sets some pairs have been placed deliberately, so the total number of qualifying pairs is going to be increased. But of course the number is going to be very variable, so you have got a background of noise of "false pairs" in determining symmetry.

When the tolerance range is small the calculation of the expected

number of qualifying pairs is straightforward, but when the tolerance range is large it becomes tricky because dots are then spreading outside the original area and the average density is non-homogeneous. So we did a computer simulation in which a series of patterns was generated, and then the computer sorted through the pairs and decided which qualified as symmetric. The line in Fig. 9, using the scale on the right, shows what value of d' the computer could achieve using this count of qualifying pairs as the decision variable. It shows no plateau with small tolerances as the experimental points do, because of course the computer can go on using whatever accuracy is available. But for large tolerances the theoretical and experimental points can be made to agree by plotting the theoretical points on a different scale from the experimental. In fact the scales differ by a factor of 2, and that means that the ideal d' is twice the experimental d' . The efficiency of utilizing the information present in the patterns is obtained by squaring the d' ratio, so in this case the figure is 25%.

For tasks of this type I have shown you that human subjects use about 25% of the statistical information. This is a fairly high figure, and we started wondering what kind of mechanisms might achieve it. The first attempt at a model is shown in Fig. 10.

We supposed that the mechanism does not work on the exact position of every dot, but counts up the number of dots in big squares and compares each with the number in a symmetric square. If the pattern was symmetric these numbers should be equal. The mechanism then calculates a statistic, which is a chi-squared test for the absence of symmetry. If chi-squared for a particular pattern is above a certain figure the mechanism says it is not symmetric, if it is below it says it is. With a computer simulation of this test we get the result shown in figure 11. The continuous line is the ideal method as described above, but now plotted on the same scale as the other points so it is much higher. The points are the experimental quantities as before, and the dotted curve is the prediction of the chi-squared model. It seems to fit rather well. And it is more convincing lying well below the ideal curve, one could argue that a lot of different methods would all have given the same result.

We should maybe have stopped at that point, but we thought we should do some additional tests of the model. The first one was to constrain the generation of the dots so there were always an equal number in each of those big squares. Well, if the model is correct,

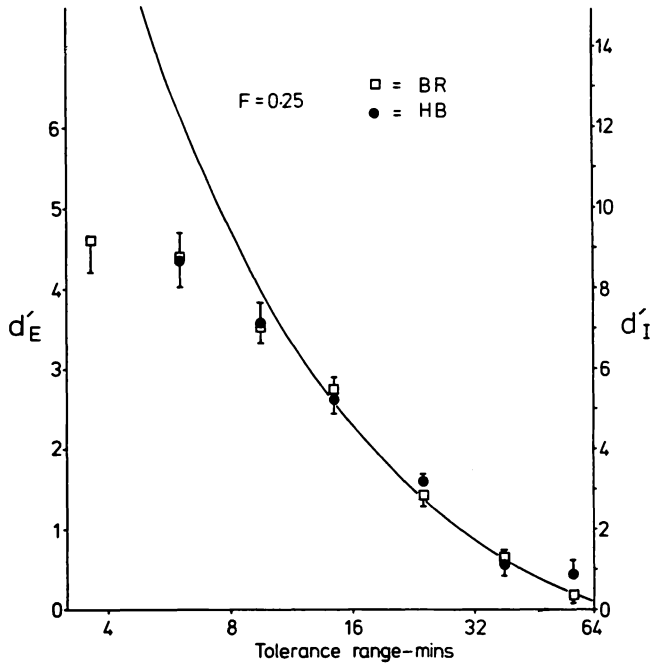


Figure 10: This first model for the symmetry detecting mechanism uses the number of dots in 16 large subdivisions of the pattern, rather than the positions of each dot. The counts in symmetric subdivisions are compared, and χ^2 calculated for the hypothesis that there is no symmetry. The performance of this model is shown in Fig. 11 (from Barlow and Reeves, 1979).

that should have abolished all appearances of symmetry, because the model says you only use the number of dots in each of these squares. That's perhaps a little bit harsh because of of course one could have had more squares overlapping without destroying the essence of the model, but the results were devastating because one could perform this task almost as well as the original one. So that wasn't very encouraging. We did some more tests; for example, we took a generated pattern and then re-randomized the dots within those squares. That again should have had no effect on performance according to the model, but it did. It reduced the efficiency from about 25% to about 1%. So again the model looks bad. We then tried replacing the array of dots in a square by a single dot whose area or whose intensity varied according to the number in that square. We did rather better on that; you could reach about 10% efficiency, but this is not as high as the 25% for the original pattern.

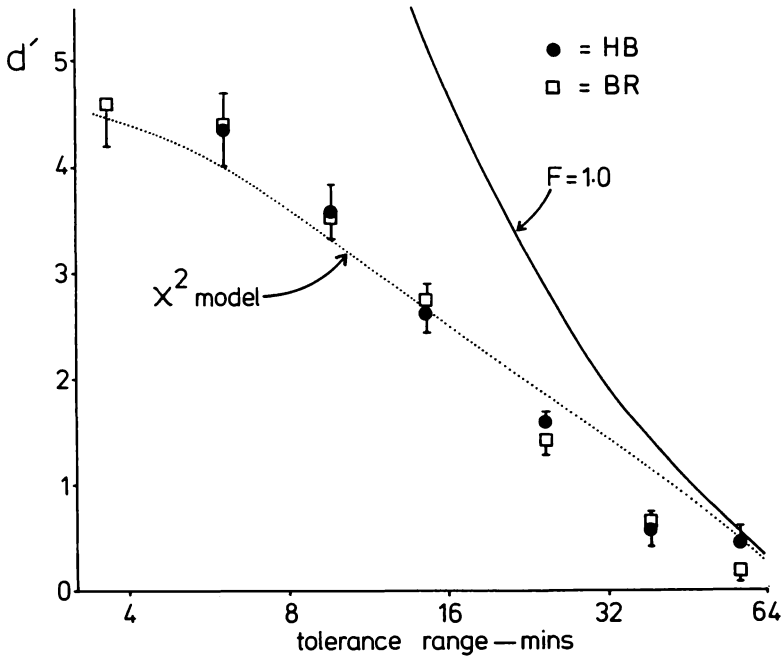


Figure 11: The dotted line shows the performance of the χ^2 model of Fig. 10. The experimental points are reproduced from Fig. 9, and the continuous line is the ideal performance curve from Fig. 9 plotted here on the same scale as d' . The model describes the performance but subsequent tests show that higher efficiencies than it predicts can be obtained; it therefore requires modification. (From Barlow and Reeves, 1979).

We were discouraged with the model at that point in spite of the good fit of Fig. 13, and decided to test out the essential features one at a time. Of course the most important feature of this model is the fact that it works at low resolution. Instead of working from the exact position of each dot, it uses the total number within a certain area. We thought it would be a good idea to try the effect of blurring these symmetric patterns; if the mechanism works at low resolution, it should do little to mar performance. So we placed a diffusing screen in front of the oscilloscope and Fig. 12 gives an idea of what the patterns then look like. These are the same patterns as those in Fig. 8, but seen through the diffusing screen. They are rather beautiful and one is strangely fascinated looking at them. They are somewhat reminiscent of cross-sections of the brain at various levels, but I hasten to say that I don't think that's significant.

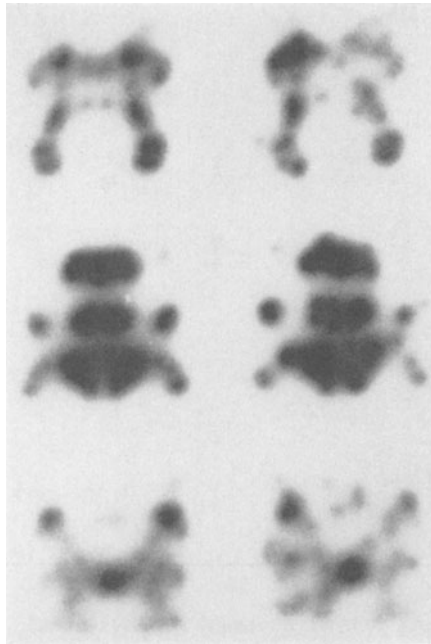


Figure 12: The appearance of the patterns of Fig. 8 when viewed through a diffusing screen. Subjects are better able to discriminate symmetric patterns under such conditions (see figure 13).

Figure 13 shows measurements of performance as a function of the width of the line-spread function produced by the screen. As expected we found performance was degraded if you have severe blurring, but the peak values are obtained with a full width at half height of 20 to 30 minutes, and even a blur of width 1 degree only reduces performance from a peak d' value 3.5 to a figure of 2.5. The fact that you require severe blurring to degrade performance seemed to be in favour of the model. But as you can see, these peak values are actually higher than with no blur at all. That was certainly not predicted by the model; any degrading effect such as that produced by the diffusing screen should mar performance, but clearly it does not.

Realizing that detection gets better with mild blurring, we repeated the previous experiment, in which we had measured performance as a function of tolerance range, and this is shown in Fig. 14. The results for small smears are unreliable, because too few errors were made, but the ones for larger smears are reliable and now the line for

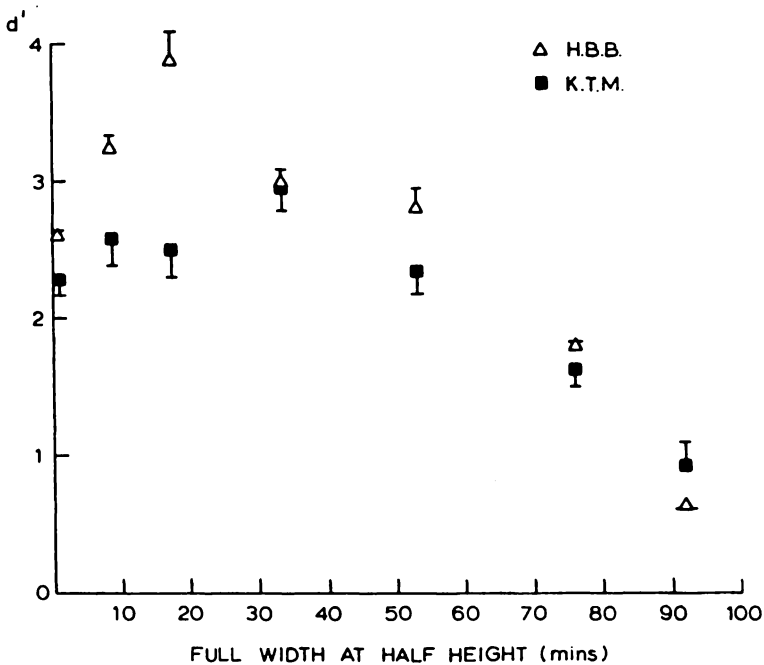


Figure 13: The effect of the diffusing screen on discriminability of symmetry. Patterns with a tolerance range of 15 mins vertically and horizontally had to be discriminated from random patterns, which can normally be done with d_E 2.5 approx. When blurring was severe, discriminability was impaired, but this only occurred when the line-spread function produced by the screen had a full width at half height of about 50 minutes or more. For moderate blurring performance was not degraded, as expected from the hypothesis that symmetry detection uses a low resolution. What was unexpected was the improvement in performance by moderate blurring, up to 30-40 min full width at half height.

50% efficiency goes through them; thus the diffusing screen has increased efficiency from 25% to 50%. That rules out completely the previous chi-squared model, which matched the points but was only 25% efficient. The virtue of using the efficiency measure is that if you get a measured performance which is above that of the model you know the model must certainly be wrong.

Well that's where we are on that particular problem. The conclusions to be drawn are that symmetry detection depends on low resolution information, but the chi-squared model of Fig. 10 is not correct and needs modifying. We haven't done that yet, but we do now

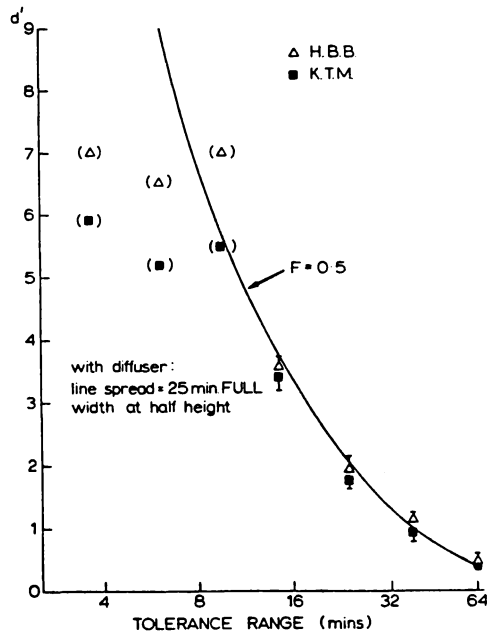


Figure 14: Discriminability of random from symmetric patterns with varying smears when viewed through a diffuser yielding a line spread function of 25 min full width at half height. Points in parentheses are unreliable because too few errors were made. For tolerance ranges of 15 mins or more the points have an estimated standard error as shown, and they indicate an efficiency of 50% under these conditions.

have quite a number of empirically determined features of the symmetry detecting mechanism which will give us some basis for putting forward a neuro-model. I think this is encouraging because detecting symmetry is something that involves the whole of the pattern, and it is remarkable that one can do it with a high efficiency.

The figure of 50% is actually as high an efficiency as I have measured for any task, even the very simplest one of detecting the absence or presence of a weak light, at threshold, where it turns out that you only use about 50% of the information (Barlow, 1977). The figure of 50% is also reached, but not exceeded, when detecting variations of dot density (Barlow, 1978). To show I have no prejudices I also did this (with Aart van Meeteren) using sinusoidal modulations of dot density, and the answer to that is the same: provided that you

don't have more than about 4 or 5 bars in the grating you perform with up to 50% efficiency. So apparently one can do this global type of task as efficiently as much simpler ones. One can visualize detecting local variation of dot density with local feature detectors and I like to think that the global task of symmetry detecting can also be done by a global feature detector along the general lines of Fig. 10, though we know that needs modifying.

I should mention a final conclusion from the high efficiencies of performance of these perceptual tasks, even though it is not so relevant to the theme of this conference. It is that the statistical limits of induction may be as important a factor for some higher perceptual tasks as physical factors, such as the quality of the image and the absorption spectra of pigments, are for simpler sensory tasks.

The Future of Feature Detectors

The first point to make is that those who explore the properties of single neurones in new parts of sensory systems, or well-known parts in new animals, are likely to need the concept of feature detectors in the future, as in the past, simply as a convenient qualitative description of experimental findings. The difficulty of discovering the specific stimulus that a particular cell demands has not been experienced by many of those who criticize the concept, and it is doubtful if they would be so critical if they had experienced it. For myself, the drama of resolving this difficulty was greatest when working with Levick and Hill on the rarer types of unit near the visual streak of the rabbit retina. One would know that the electrode was near a ganglion cell from the occasional, accidentally elicited, action potential, and one would know whereabouts in the visual field the receptive field lay from the position of the electrode on the retina and from the previously plotted fields; but it might take an hour or more of frustrating trials before one discovered the stimulus that gave reliable, vigorous responses, and it was because of the drama of ultimately firing the cell reliably that we coined the phrase "trigger feature" for the appropriate patterned stimulus. Of course not all units are hard to trigger; some respond to an extended stimulus such as a line or edge of any orientation, and these are easy to track down. But if they require slow movement, or small size, or critical orientation, a rapid search is impossible.

The terms trigger-feature and feature-detector are useful for the qualitative description of units which are highly selective, though

more quantitative descriptions are desirable and will, I have no doubt, come to be used more and more. However I personally shall continue to find a reliable qualitative description of a new type of selectivity more important and interesting than the quantification of established types.

Could one find feature detectors by other means than single-unit recording? The development of activity-sensitive anatomical methods such as the de-oxy-glucose technique raises fascinating possibilities, but of course the time scale of exploration is likely to make the discovery of new trigger-features impossible; one would never have thought of examining the cortex with this technique following uniocular exposure, or following exposure to striped fields (Hubel, Wiesel and Stryker, 1978) without the previous single unit results.

I mentioned at the beginning of this talk that the notion of "releasers", derived from ethological behavioural studies, had given an initial impetus to the discovery of feature detectors, and perhaps this source of discovery may not be exhausted. Those types of sensory stimulus that elicit distinct behavioural effects are also surely more likely to give definite neural responses. For example a combination of the ethological and the histological approaches might enable one to stain those cells in the visual pathway that are activated when a chick responds to a stimulus to which it is imprinted. At early levels activity can presumably only be triggered by stimuli for which the chick is endowed with feature-detectors, while at a higher level still activity should be aroused only by imprinted trigger features or combinations of trigger features. This is no more than fantasy, perhaps, but it is certainly stupid for physiologists and anatomists to neglect the possibilities suggested by behavioural studies.

Thus I think feature detectors definitely have a future for experimentalists, but is the concept also useful for those trying to understand and theorise about higher nervous function? Here again I think the answer is yes, and I will make this point in the form of the following, possibly controversial, postulate: The sensory performance of the whole animal is never better than that of at least one of its feature-detecting single units. The word "better" above is too broad, because the whole animal can certainly respond in a more versatile way than any one of its feature detectors, and it should be understood to mean "more efficient" in the statistical sense already explained. What

is intended is the claim that if an animal reliably reacts differently in two situations, somewhere in its brain there must be at least one nerve cell that reliably responds differently in the two situations. The response is not necessarily always based on the same neurone, but the response of the whole animal to the whole set of situations can be no more reliable than the response of each single neurone to the subset of stimulations that it discriminates.

Clearly the future here lies with computer modelling, and I would be quite happy to see the term "feature detector" replaced by various types of linear operations and categorical descriptive terms in these representational models.

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