

Perception: what quantitative laws govern the acquisition of knowledge from the senses?

H. B. BARLOW

Soon after I started physiological research I was lucky enough to make an interesting, but as it turned out unoriginal, discovery (Barlow 1950). I was repeating some experiments that Hartline (1938, 1940) had done on the frog's retina, with the idea that the very large receptive fields¹ he had discovered might not be simple spatial integrators of light, as he had suggested, but might have some form of pattern selectivity. The experiment was to measure the threshold for eliciting impulses from a retinal ganglion cell as a function of the area of the stimulus spot. If spatial integration occurred, and the sensitivity over the receptive field was uniform, there would be a simple linear relation between sensitivity (the reciprocal of threshold) and the area of the receptive field covered by the spot; if, on the other hand, the ganglion cell responded selectively to the edges of the spot, then a square root relation might be found because the circumference of a spot varies as the square root of its area, and this was what I was hoping for. Figure 2.1 shows what happened: the sensitivity rose pretty well according to the line predicted from complete summation of the sensitivities of the regions covered by the spot, as determined by previous measurements on the receptive field, and as Hartline had said it did. It is true that the experimental points lay a bit below, especially as the spots spread out over the weaker parts at the edges of the receptive field, but on these double logarithmic coordinates the slope should have been about one half if the square root law I had hoped for was followed, and I could not pretend it was as low as that. As I gloomily pondered over this result I noticed that when the spot spread outside the limits of the receptive field I had plotted, the sensitivity fell off steeply. Though it was not what I was looking for, this rise of threshold was actually just what my

¹Hartline dissected out and recorded from optic nerve fibres coming from ganglion cells in the retinas of frogs and other animals. He defined the 'receptive field' of a single fibre as the region of the retina to which light had to be applied to elicit action potentials in that fibre. These receptive fields measured about 1 mm in diameter, and those of neighbouring fibres overlapped each other to a huge extent.

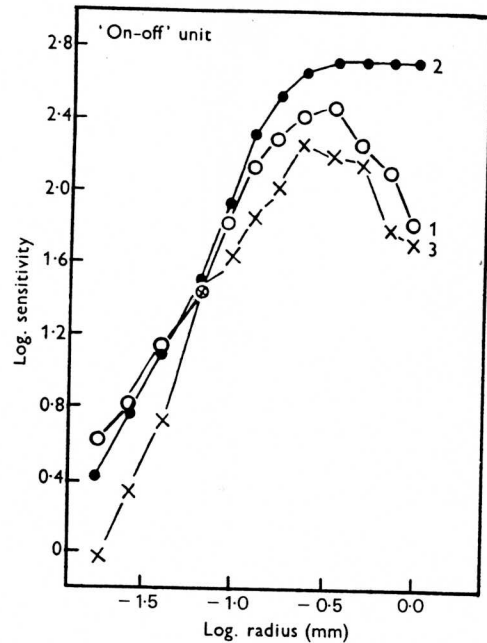


Fig. 2.1. Evidence for lateral inhibition from area-threshold curves. If this 'on-off' type ganglion cell in the frog's retina integrated the stimulus light, weighting it according to the sensitivity profile of its receptive field (Hartline 1940), the sensitivity (1/threshold) to stimulus spots placed centrally within that field would rise with radius according to the curve indicated by black dots (curve 2). The local sensitivities for making this prediction were determined with a small spot at a matrix of positions covering the whole receptive field. Circles (1) and crosses (3) show the actual values obtained with centrally placed spots of varied radii before and after the small spot determined a linear relation between radius and sensitivity (that is, square root relation between area and sensitivity) would be expected if the ganglion cell responded to edges, and this would have a slope half that of curve 2, close to unity on these double logarithmic coordinates; the ganglion cell clearly follows Hartline's prediction of linear summation, at least below about 0.2 mm radius. However at large radii threshold values rise rapidly and sensitivity falls a long way below the prediction for linear integration (curve 2). This fitted the edge-detecting hypothesis, but Fig. 2.2 gives a simpler explanation in terms of lateral inhibition (from Barlow 1950, 1953).

hypothesis predicted, for if the ganglion cell responded only to the edge, it would clearly be insensitive when the spot had expanded and its edge lay outside the receptive field. But I was wrong again and there was a simpler explanation. A spot of light falling outside the receptive field does not, by definition, excite the ganglion cell either when switched 'on' or 'off', but as Fig. 2.2 shows, it powerfully inhibits both the 'on' and 'off' responses elicited by a spot within the receptive field (Barlow 1953).

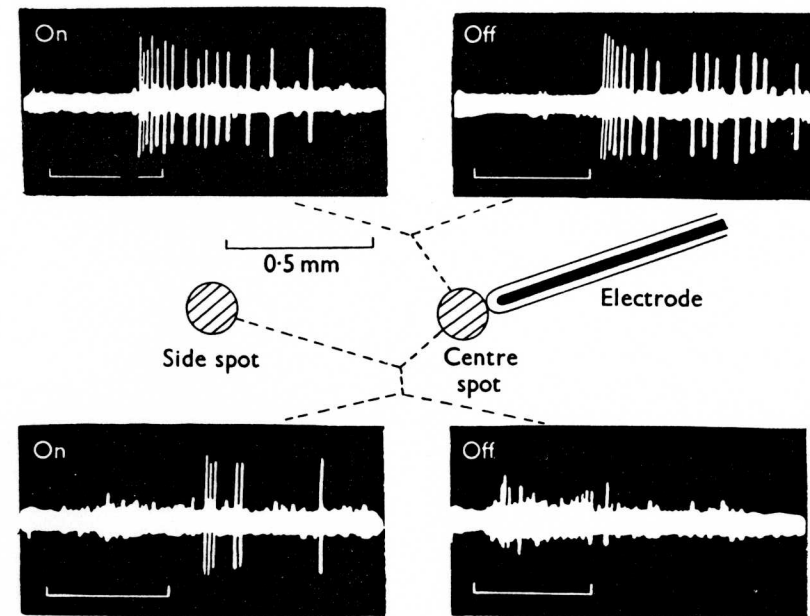


Fig. 2.2. The spot projected near the tip of the electrode was at the centre of the receptive field of an 'on-off' type ganglion cell in a frog's retina. When it was turned on and off the pair of responses at top were obtained. A second spot placed about $\frac{3}{4}$ mm away from the centre produced no response at all by itself, but when turned on and off synchronously with the centre spot it caused the responses to be much reduced, as shown in the lower pair; regions outside the receptive field can inhibit responses evoked inside it. This second spot is at a position corresponding to the outer edge of the largest spot used in Fig. 2.1, and this type of inhibition must be responsible for the drop in sensitivity with large spots shown there (from Barlow 1953).

The discovery of lateral inhibition, or 'surround suppression' as this form of it is perhaps better named, was unoriginal for two reasons. First, Hartline had described it in *Limulus* the year before (Hartline 1949). And, second, it was clearly anticipated by Johannes Muller 112 years earlier, when he spoke of 'the reciprocal action of different parts of the retina upon each other'. But I was very excited because the ability to record from single neurons in sensory pathways did seem to get the physiologist's foot inside the door of psychology, and my foot has been stuck there ever since.

To begin with, what I saw through the door appeared hopelessly uncongenial, but that had more to do with the question usually asked by psychologists than the answers they found. Thus Koffka (1935) said that the aim of the gestalt school was to explain 'Why things look as they do', and this aim was recently repeated by Hochberg (1978). It seems to be accepted as the aim

of research into perception, not only by philosophers and laymen, but also by many students of psychology even today. But it is an amazingly restricted objective; imagine a physiologist being told that the aim of research into reproduction is to explain why being in love feels as it does! He would be concerned with much more earthy matters, and if subjective feelings were discussed at all, they would be regarded merely as a byproduct in the physiological process of reproduction. Of course feelings do have some interest in their own right, but all the same a physiologist is bound to regard 'the way things look' as little more than a byproduct of the process whereby the brain makes use of sensory information.

The difference between the two approaches can give rise to serious misunderstandings: if a physiologist calls an orientationally selective cell in the cat's primary visual cortex an 'edge-detector', a phenomenologically tainted psychologist may think he implies that similar cells give rise, more or less directly, to the subjective experience of an edge in humans. All he really meant was that cells of this type play a role in detecting and classifying edges comparable to that of cones in colour vision: they are the first cells in the pathway with the type of selective sensitivity that would be capable of discriminating edge orientation in the first case, or spectral composition in the second. The physiologist's objective is not to explain subjective experience but to account for the action of the brain in physical and chemical terms, and I at least do not know how subjective phenomenology can be so expressed; though it is tempting to speculate, it would surely be foolish to invest much capital in a currency with an undefined, and perhaps undefinable, exchange rate.

What work is done in perception?

For a physiologist studying an organ or system the first problem is to specify what it achieves. What useful work is done in perception? I rather think an old-fashioned psychologist would find this a fatuous question: perceptual mechanisms give rise to our experiences of the world around us, and what more can you possibly say about their functional role? But as it happened, J. J. Gibson (1950) published his first book in the same year that I repeated Hartline's experiment, and I think this started to change the climate of opinion. Though Helmholtz and Kenneth Craik certainly appreciated it long before him, Gibson seems to have apprehended more clearly than his contemporaries that the task accomplished in perception is an extraordinarily complex and difficult one. This had been borne in on him during the war when he was studying the perceptual problems of those learning a practical skill such as landing a plane on the deck of an aircraft carrier; in such conditions a gestalt principle like that of 'good continuation' is altogether too vague and optimistic a guide for deciding what specific features should be

attended to. We have since learned that the cues to the third dimension that he pointed out, such as texture gradients, converging contours, relative motion, and so forth, are themselves none too easy to extract from transient and unstable visual images, but his was the first step in the right direction: after him, psychologists understood that the main question is not 'Why things look as they do' but why it is that the way things look is usually the way they actually are, as confirmed by touching them, or successfully landing a plane on them. The trouble is that our eyes acquire this reliable knowledge of our surroundings with such complete absence of conscious effort that one needs to be reminded that a complex and difficult task is necessary; an example from hearing may illustrate this.

Everyone knows that sound is transmitted as a rapidly fluctuating air pressure. Figure 2.3 shows two waveforms: the top one was obtained during the utterance of one word, the lower one during another. You can see at a glance that each word has a complex waveform containing a lot of information, but I doubt if the experts can say what the words are, or even identify

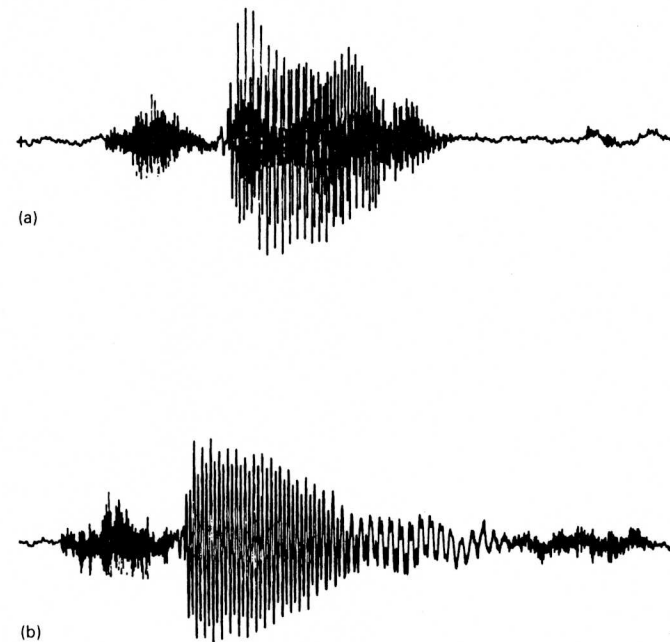


Fig. 2.3.(a) and (b). Two complex waveforms that can be identified instantly and unambiguously when listened to. Visually it is by no means obvious which is 'chalk' and which 'cheese', so one's auditory perception must perform a quite complex analysis (chalk is the top one). The waveforms each last half a second and were kindly provided by R. Fettiplace.

