PROPERTIES OF PLASTIC NETWORKS

A. M. UTTLEY

From the National Physical Laboratory, Teddington, Middlesex, Great Britain

INTRODUCTION

For the last twenty years there have been determined attempts by biologists and engineers to cooperate in the study of the nervous system. There has been some progress in our understanding of innate, non-plastic behaviour; here the theory of logical networks can be applied to a considerable extent. But, so far, plastic behaviour remains largely unexplained. The paper reviews briefly the work of Turing, Von Neumann, McCulloch, Pitts, Uttley and others on the application of switching theory and logical computer design to problems of innate classification of stimuli and synthesis of fixed motor patterns. Storage is not required in such mechanisms.

Aims in the theory of plastic networks

In general terms the task of an engineer is to design a machine to have a given performance. The specification of behaviour comes first; for it the engineer has to deduce the necessary functions, and then to design equipment capable of performing them. The reverse process would arise if an engineer were presented with a novel machine and asked what it was for. This is a most unusual and uncertain procedure, particularly if the machine lies outside the experience of the engineer.

By analogy it is suggested that the engineer can best help, in the study of the nervous system, by studying known psychological facts of behaviour and attempting to devise mechanisms which will have such behaviour; his proposals may be regarded as physiological theories of neural mechanism. The engineer's theories will be of value only if they can be tested physiologically. Because of the language difficulty between psychology, engineering and physiology, it is very helpful if working models can be built; they form a check of the practicability of the engineer's theory and they form a kind of universal language between the three sciences.

Mathematicians and engineers are addressing themselves to a number of specific problems:

1. Simulation of learning to associate one sensory stimulus with another (classical conditioning, S-S learning) and hence to predict further stimuli.
2. Learning by trial-and-error motor activity, what kind of action R will have the

greatest chance of giving rise to a goal G in a particular situation S. (S-R learning).

3. Recoding highly redundant stimuli into less redundant signals.

4. Adaptive classification whereby a system of reasonable size can classify with decreasing error on a basis of (a) frequency of occurrence and (b) association of members of a class with some label, sign or symbol.

LOGICAL NETWORKS

Turing (1936) and Von Neumann (1945) showed that a digital computer could be designed to perform any mathematical or logical function by connecting together units of limited type and with an input which consisted of binary numbers only. All the sixteen possible logical functions of two binary numbers can be derived from a carefully chosen pair of them; for example AND and NOT are sufficient, where (A AND B) is given by the table

	B 1	0
A		
1	1	0
0	0	0

and (not A) is given by

A	NOT A
1	0
0	1

Turing pointed out that a simple mechanism for AND, which might exist in neural structures, would be a "threshold of 2" units with two inputs and one output, the output being 1 if both inputs were 1. He also pointed out that an inhibitory unit was essential if the brain were to compute logically; this was also a unit with two inputs A and B and one output O; but the output O must be 1 only if A were 1 and B were O. The two units are shown diagramatically in Figs. 1a and 1b.

An OR unit would be formed if there were two inputs, and if the threshold for an output were 1.

Von Neumann (1956), McCulloch and Pitts (1943), and Allanson (1956)

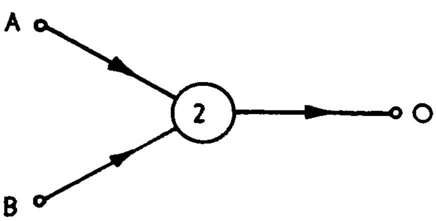

FIGURE 1a *A* and *B*

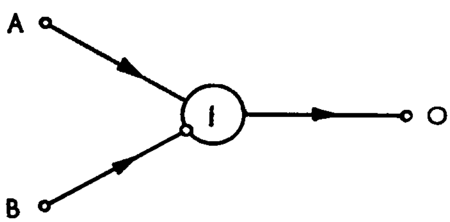

FIGURE 1b *A* and not *B*

have considered the performance of unreliable units in which there is only a probability that the output of a unit will be correct. Considering only the AND unit we may regard it as a connection from A to O which is made by changing B from O to 1. Suppose that a number of such units are connected in a hammock-like way, as in Fig. 2, each with a B input; then if some of the links fail to make when B becomes 1, there can still be a connection from A to O.

Classification

A particular form of logical computer is capable of classifying the signals which may occur in a set of binary input channels (Uttley, 1954). A classification system with three input channels is sketched in Fig. 3.

There are units connected to the inputs in all possible ways, one at a time, two at a time and three at a time; the function of each unit is to indicate if all the inputs connected to it are active simultaneously. Comparing the input signals to notes in music, each unit distinguishes a particular chord, though regardless of the presence

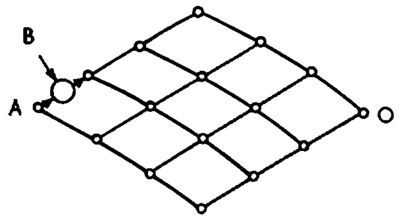

FIGURE 2 A network of unreliable *AND* units forming a more reliable *AND* unit from *A* to O

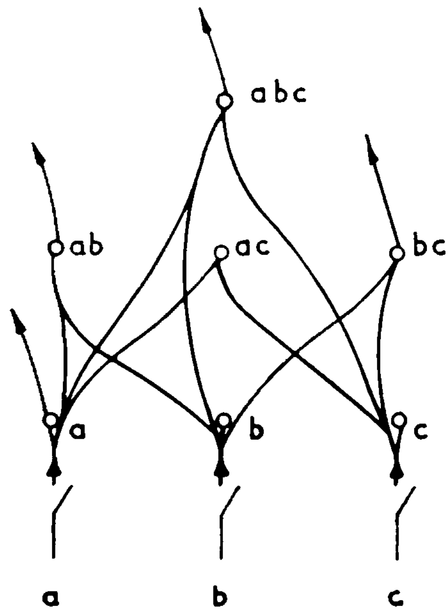

FIGURE 3 A complete classification system for three binary inputs.

of additional notes (properties); in a system with, say, seven inputs *a* to *g*, the (*bcd*) unit will indicate if there is activity, for example, in the set of inputs (*bcd*) (*bcdf*) or (*bcdeg*).

A set of properties will be called a *pattern,* and in line with the terminology of Set Theory, if one set of properties contains another set it is called a superset of it. The corresponding indicating unit will be called a superunit of the unit which indicates the contained set.

If a two-dimensional array of light receptors were connected to a complete classification system there would be an indicating unit for every distinguishable shape; such a system could not, of course, generalize in respect of size or orientation.

In a system with complete classification, inputs would be connected to units in all possible ways and the connexions would show no particular structure; they could, indeed, arise from a principle of random growth. On the other hand, a classification system could be designed with special connexions to distinguish certain patterns only; Fig. 4 shows such a system, which distinguishes only the patterns (*abf*), (*df*)

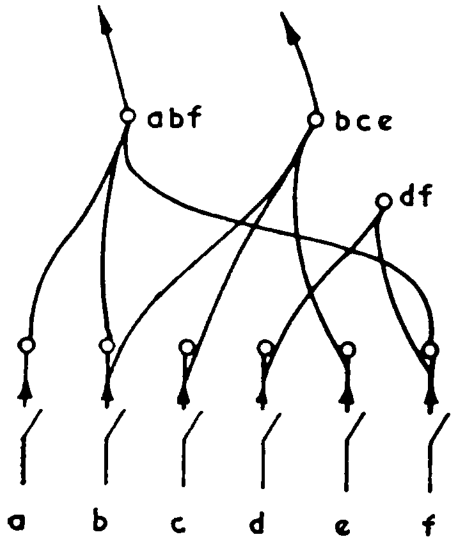

FIGURE 4 An incomplete classification system for binary inputs.

and (*bce*). It is suggested that it is such a special classification system which gives rise to Innate Releaser Mechanisms (Tinbergen, 1951).

In a classification system a complex pattern of input signals activates a single key unit which corresponds to that pattern. Such a system can operate in the converse manner, as in Fig. 5 where the units form the input points; if any one unit is activated, a complex pattern of activity will occur at the lowest level of the system and this can form the output of the system. The classification principle is used here to synthesize patterns rather than to analyse them; by such means innate response patterns may be evoked.

Classification systems can be constructed entirely from Turing's AND units as in Fig. 6 or, indeed, from units with any fixed threshold greater than unity. By adding inhibitory units it is possible to prevent an (*ab*) unit, for example, from indicating when a greater pattern, such as (*abc*), occurs. There would appear to be no difficulty, in principle, of understanding how stimuli of a certain class give rise to motor patterns of a certain class in a deterministic manner in animals.

For example, Hassenstein and Reichardt (1956) have considered the behaviour

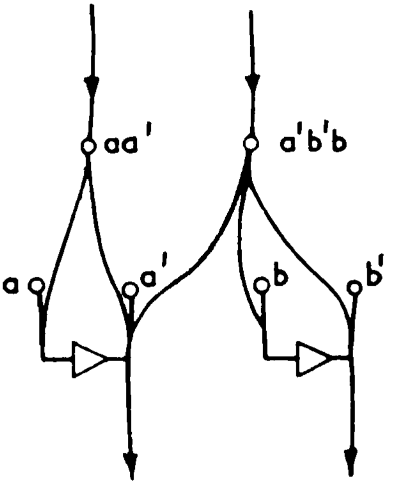

FIGURE 5 A classification system for synthesizing spatiotemporal patterns. ▷ notes delay.

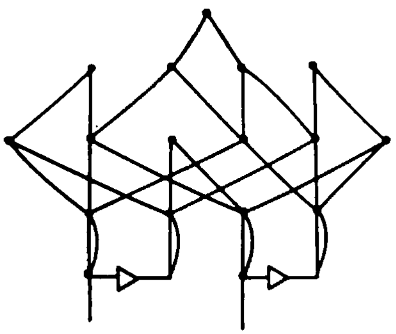

FIGURE 6 A classification system constructed of identical units with a threshold of two input signals.

of a beetle (Chlorophanus) when turning to face a moving seen object. They postulate visual cells which discharge when their illumination decreases—off-centre units (Hartline) and other visual cells which discharge when their illumination increases—on-centre units. They also postulate a mechanism D for delaying signals.

Suppose that a dark boundary of an object moves from left to right; this can be detected by the mechanism of Fig. 7 which can emit a motor command "turn right."

A complete system for turning right or left towards dark or light moving objects is shown in Fig. 8.

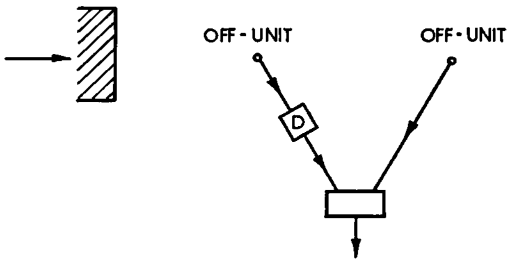

FIGURE 7 A logical circuit for detecting the movement of a dark boundary from left to right. Off-units emit signals when illumination decreases. D is a delay unit.

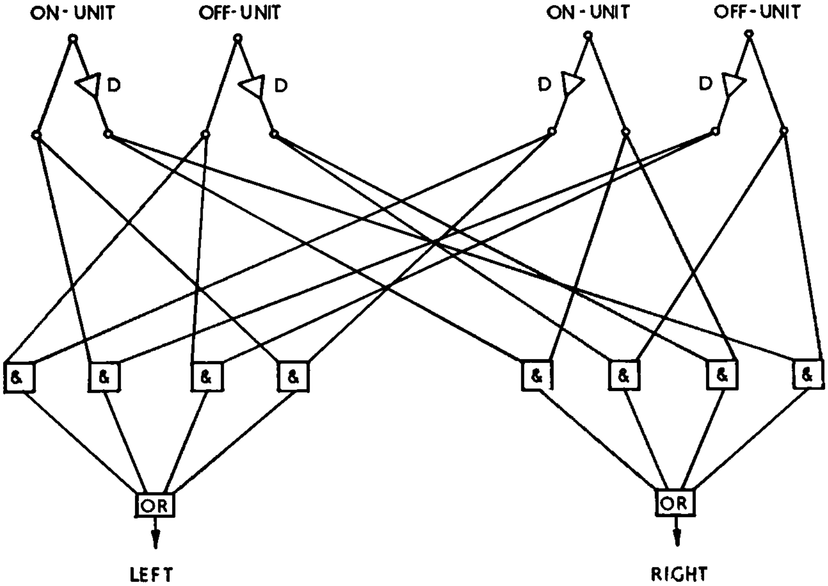

FIGURE 8 An extended circuit for detecting movement left or right of light or dark objects.

PLASTIC NETWORKS

Because a classification system possesses no storage, its behaviour depends only on the present input. If storage is introduced, then the output of a system can depend not only on the input signal but also on the stored quantities; the way is then open to the study of plastic behaviour in animals.

The earliest attempts in this direction were those of Grey Walter (1951) and Hull, who made models which demonstrated some of the properties of classical conditioned reflexes. Here, a conditioned stimulus S_c, the sound of a bell for example, is associated with an unconditioned stimulus S_u, the taste of food for example;

the latter stimulus causes salivation in a nonplastic, deterministic manner. In these models a counter stored the number of conjunctions of the two stimuli, and when this number exceeded a threshold a connexion was made between the units which discriminated the two stimuli.

Conditional Probability

Uttley (1956a) showed that such a system could not simulate the extinction of a conditioned reflex which occurs when the conditioned stimulus S_c is given without reinforcement of the unconditioned stimulus S_u. He pointed out that a second counter was required for the conditioned stimulus. The fraction is the conditional prob-

$$\frac{\text{Number of conjunctions of } S_c \text{ and } S_u}{\text{Total number of occurrences of } S_c}$$

ability that S_c will be followed by S_u; and this quantity closely mimics very many properties of classical conditioning. Trial-and-error learning can be imitated in such a system (Uttley, 1956b).

If the classification system of Fig. 3 is given some additional properties it becomes a conditional probability system which can, from past events, compute the probability of one stimulus being followed by other stimuli.

Each unit must change its state after indicating and, as a result, there must be two after effects (Uttley, 1959).

(1) The output signal of each unit must change in size. The simplest law would be that, after counting N times, the output signal became K'/N.

(2) The sensitivity of each unit to received signals must change. Again the simplest law would be for the sensitivity to be equal to KN.

Now consider only the two-input systems of Fig. 9.

If S_c has occurred ten times, of which the last four have been accompanied by S_u, then the counters of the three units will contain the numbers shown in the figure.

If S_c now occurs alone, the signal from S_c will have strength K′/10 and the sensi-

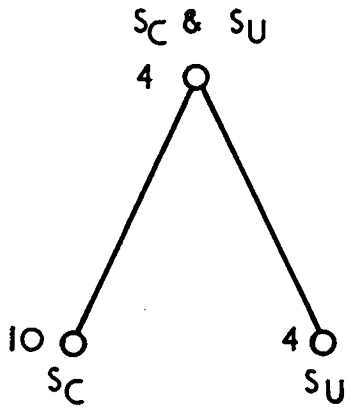

FIGURE 9 A conditional probability system for two binary inputs.

tivity of the (S_c and S_u) unit will be 4K. As a result, the effect of the signal S_c on the upper unit will be $\frac{4}{10}$ KK′ which is proportional to the probability of S_c being accompanied by S_u.

Although the theory explains many forms of animal behaviour there are a number of physiological difficulties regarding its functioning. Firstly, the requirements that, after firing, a neuron shall become a less sensitive transmitter and a more sensitive receiver are the reverse, respectively, of post-tetanic potentiation and adaptation; there is evidence (Burns, 1961) that the sensitivity of a cortical neuron is reduced after firing (adaptation). This difficulty can be met by reversing the scale upon which probabilities are represented to a negative logarithmic one. Outputs due to events are then strictly proportional to their information gain so that there is a large output for the unpredicted event and no output if the predicted event is completely certain.

The negative logarithm of probability will be called Rarity and the changed system a Conditional Rarity Computer.

The necessary laws of synaptic transmission then became:

(1a) After a neuron has fired it becomes a less sensitive receiver at all its dendritic synapses (adaptation).

(2a) After a neuron has fired it becomes a more powerful transmitter at all its axonal synapses (post-tetanic potentiation).

The prediction 1a has been found to be true (Burns, loc. cit.). The prediction 2a awaits confirmation; there are some preliminary experiments which indicate that this may be so. (Burns, 1961).

It can be seen that, in such a neural system, experimental findings could easily seem to be conflicting, some supporting facilitation—some adaptation, if the changes in state of a synapse were thought of in terms of one variable rather than two.

Overconnected Networks

The greatest difficulty of a pure conditional probability theory is that it demands 2^n cells for an input of n binary channels; this is not only an impossibly large number for a nervous system of say 10^6 inputs, but it gives instantaneous discrimination of all possible patterns—and this does not occur in animals; they slowly learn to discriminate. One is led to wonder whether a system could operate on the principle of holding available a set of unconnected units and, by some plastic process, connecting them up for those patterns which do in fact occur frequently in a particular environment. This gradual increase in connectivity would demand the often-postulated principle of facilitation whereby use increases conductance; but it can be shown to be illogical.

Consider the simple situation of two channels a and b with an indicating unit for each and a third unit available for connexion if, in fact, a and b ever do occur together. The requirement now is to close the switches which connect the *ab* unit to the *a* and the *b* units if *ab* often occurs. Clearly an *ab* unit is required to detect whether *ab* does occur. The proposal results, not in economy, but in a duplication of units. The same basic illogicality shows up in the facilitation theory. If, initially, the conjunction *ab* does not occur and no impulses travel from, say, the *a* unit to the *ab* unit, then the principle that the passage of impulses facilitates conduction between units can never begin to operate.

However, these illogicalities disappear if the converse principle is used. Suppose that units are initially overconnected, rather than underconnected, so that there is great ambiguity of discrimination. The ambiguity will be reduced if, by use, connexions become less effective; this demands adaptation, a widely occurring physiological phenomenon. As the connectivity is reduced unambiguous classification will be achieved.

Consider a classification system consisting of a large number of neurons, each with a fixed threshold, *i.e.* such that it will fire if more than a small fixed number, r, of its inputs are active. Suppose also that each neuron has R inputs where R is much greater than r. The number of possible input patterns to each unit is 2^R and a negligible number of these—those with less than r elements—will fail to fire the neuron. The ambiguity of discrimination of each unit may be said to be about 2^R.

If there are N such neurons there will never be more than N distinguishable patterns even if variation of threshold is introduced; but, in principle, such a system should be capable of adapting itself to discriminate N patterns from a much wider group of $N \times 2^R$ patterns. This number could be a sizeable fraction of the total number of 2^n patterns which could arise if there were a total of n inputs to the entire system.

Suppose, now, that a neuron is given the chosen property of being a more powerful (axonal) transmitter and less sensitive (dendritic) receiver after firing. Suppose also that, of all the 2^R sets of inputs which might occur at the input to the neuron, one set occurs far more often. Then these axons will become more powerful relative to the others and as the neuron becomes less sensitive only they will fire it. The ambiguity will have been resolved.

Statistical treatment of plastic networks

R. L. Beurle (1956) has developed a theory of cortical activity in which he considers nerve tissue macroscopically, in contrast to Uttley's theories of the behaviour of individual cells.

First, he considers cells with a fixed threshold and with random connexions falling exponentially in density with distance from the cell body (Sholl, 1955); if a sheet of such cells is stimulated at a single point then a wave of activity will be propagated with a well defined front. If two such points are stimulated within a short time of one another the two waves will reinforce one another, the combined wave travelling further than either separately. Beurle then introduces storage in cells in the form of a reduced threshold after firing; he says

"If the additional cell property of *reduction of threshold* with use is postulated, further interesting properties of the medium in the presence of more than one wave arise. This additional cell property, and the complementary one of cell growth being dependent on use, have been considered previously in relation to a single wave travelling through a composite cell mass. It is perhaps easiest to discuss the effect of this property on two waves in relation to two waves crossing each other obliquely. Suppose A and B in figure indicate two wavefronts W_A and W_B which have on many occasions travelled across the region shown in the same time relationship. Then everywhere within the region shown there will be cells which, because they have been used during the passage of the waves, will have correspondingly decreased their threshold. These cells will be uniformly distributed with a density M_0 throughout the region except along the centre line L where, due to the interaction between the waves, a very much greater proportion of cells will have been used and will have decreased their threshold. As a result the critical value M_0 will be lowered all along the centre line L. The passage of one wave alone, e.g., W_A, will then produce a peak of activity where the wave intersects the line L, and if the local value of M_0 has been reduced sufficiently the peak will regenerate a second wave W_B' as it travels along the line L (Fig. 10b).

The regenerated wave, W_B', although of the same form as W_B, will not have exactly the same constitution. The constitution will, however, be similar, since the majority of cells becoming active along the line L will after many simultaneous occurrences of W_A and W_B be the same whether W_A and W_B are both present or W_A only is present."

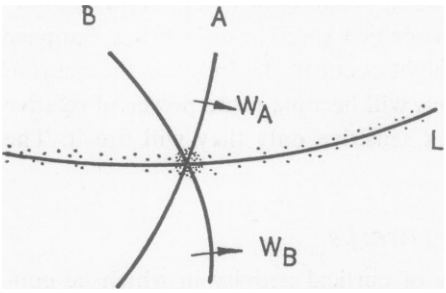

FIGURE 10a Interaction between two waves. (Beurle, 1956)

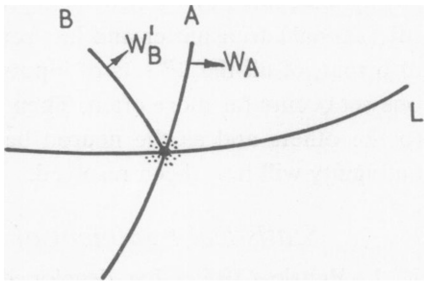

FIGURE 10b Regeneration of a wave.

PLASTIC CLASSIFICATION

There would appear to be only two ways by which a computer might *learn* to discriminate input patterns. The first is based on redundancy and the second on the use of symbols.

Redundancy

If some patterns of input activity occur more frequently than others, then the inputs are not all statistically independent. Shannon gave the name of redundancy to such a state of affairs; he showed that it is possible to recode a set of redundant signals into fewer channels containing non-redundant independent signals. If such a step is taken, a smaller classification system will be needed for discrimination of patterns.

However, if the relative frequencies of different patterns change it is necessary that the re-coding device change also. Barlow and Donaldson (1958) have constructed a system for two inputs which uses plastic coding to reduce redundancy. In their model, two binary inputs A and B are coded into six signals for each of which there is a counter. The signals are

1. A	2. not A
3. B	4. not B
5. A identical to B	6. A different from B

The least frequent of 1 and 2, 3 and 4, 5 and 6 are selected and named K, L and M respectively. The two least frequent of these quantities are transmitted. It can be shown that any such selection forms a reversible code, so that the state of the input can always be calculated from the output; no information is lost. This model chooses the code for which the number of output signals is a minimum. The economy is therefore in channel capacity rather than in the number of channels used. An important consequence of this particular form of coding is that the two output signals are less correlated than the two input signals. If a classification system is attached to a set of channels containing correlated signals then some patterns will rarely occur and so, some units of the system will rarely be used. Some preliminary coding of the above form would therefore be of value, in that the subsequent classification system would be more efficiently used.

Barlow (private communication) has suggested that correlation between signals in adjacent fibres can be reduced if they terminate among cells which they can excite but which are mutually inhibitory. If any one fibre is active it will excite such cells which will, in turn, prevent any neighbouring fibre from having excitatory effects, if it is active at the same time.

In the section on overconnected plastic networks it has been shown that a conditional rarity system, with n inputs and N units with variable connections, can adapt itself to discriminate the N most frequent of all the 2^n patterns which could occur. Again, use is made of the existence of redundancy, in that N patterns are far more frequent than all others; little information will be lost when an infrequent pattern occurs occasionally without being discriminated. In contrast to the plastic codes of Barlow and Donaldson, the overconnected conditional rarity system uses redundancy in the input to effect an economy of *units* rather than in the channel capacity of the units. The mean firing rate of cortical neurons is of the order of twenty per second which is a low figure compared with rates measured in the mid brain. It is the writer's view that economy of units in the cortex is of great importance and that economy of channel capacity is not.

The attaching of symbols to patterns

The second principle is the labelling of examples of a class of inputs by means of a symbol, the labelling being done by a "teacher" external to the system. Future discrimination then becomes the straightforward problem of "predicting the symbol."

The process is illustrated in Table I.

TABLE I

Inputs					Symbols	
a	b	c	d	e	A	B
1	1	1	0	0	1	
1	0	0	0	0		
0	0	1	0	0		
1	0	1	0	1	1	
0	1	1	1	0		1
0	0	1	0	0		
0	0	0	1	0		
0	0	0	0	1		
0	0	1	1	1		1
0	1	1	0	0		
0	0	1	0	1		
1	0	0	0	1		
					Probabilities	
1	0	0	0	0	2/4	0
0	0	1	0	0	2/4	2/4
0	0	0	1	0	0	2/3
1	0	1	0	0	1	0
0	0	1	1	0	0	1

The input pattern has five properties, and there are two symbols. Of twelve examples of the input pattern four have been labeled. In the lower half of the table unlabelled examples of increasing complexity are given; conditional probabilities of the symbols are calculated, from which it is clear what makes an A an A.

Such a system should be called "teachable"; it is not learning for itself. If, however, the external "labeller" is not an intelligent teacher but the external environment the system can "learn for itself" facts about this environment. For example, in a living organism the inputs might be commands to muscle groups and the symbols A and B might be "Food" and "Pain" stimuli. The system can then discover for itself the classes of motor pattern which are likely to precede food and pain.

The plasticity introduced in the Conditional Probability theory took two independent forms, increased output from a cell with use and increased threshold of incoming signals with use. Beurle postulated only one factor—decreased threshold with use. Selfridge (1958), Minsky (1958), and Rosenblatt (1958), in different one-variable theories, postulate only variation in the size of signals sent from one cell to another. In Selfridge's "Pandemonium" and Rosenblatt's "Perceptron" there is growing discrimination of stimuli in a plastic network, by means of a "teacher" external to the network which informs it as to the correctness of its decisions. This takes the form of increasing the size of signals which occur when the decision of the computer agrees with that of the external teacher, and conversely.

The basic principle of these machines is shown in Fig. 11.

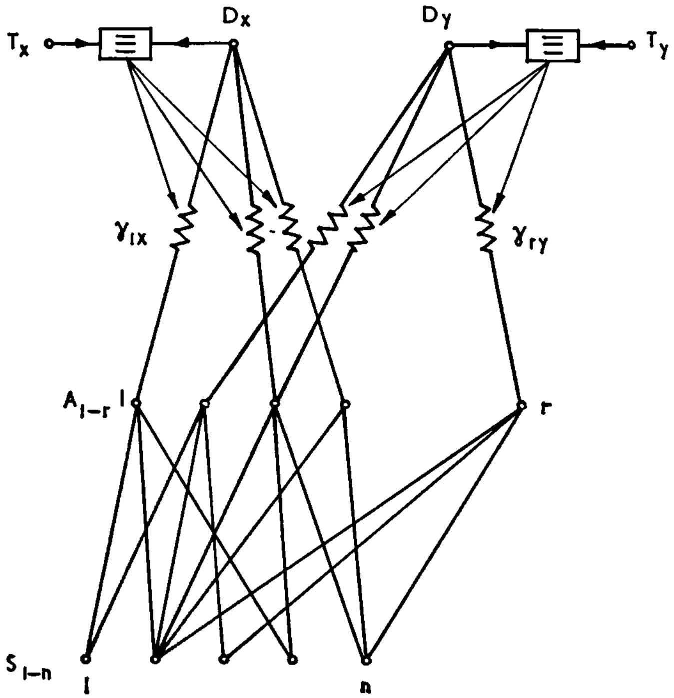

FIGURE 11 Facilitation principles underlying Pandemonium and Perceptron Systems. *S*—binary receptors. *A*—association units. *D*—decisions units. *T*—teaching inputs. γ—represents variable conductance.

An array of receptors *S* are connected randomly, in a many-to-many fashion, to a set of *A* cells which are connected in a random way to decision units D_x, D_y etc. The signals from *S* to *A* are binary but the signals from *A* to *D* are variable. The outputs at *D* are binary. All cells have a fixed threshold.

A pattern of activity *x* is presented to the receptors *S* and some of the *D* cells may become active. An external teacher "tells the machine" that x has occurred by activating the point T_x. If D_x has fired, an "identity" unit between T_x and D_x becomes active and makes important changes in the size of signals to be emitted from the A cells. It increases the signals from those A cells which are connected to D_x and which have contributed to a correct decision. It decreases the signals from those which are connected to D_x and have contributed to an incorrect decision; *they may even go negative.* The same process occurs at D_y when a pattern of activity y occurs at S. It will be seen that there is some conflict at A cells such as that marked with an asterisk.

Papert (1960) has given a particularly clear description of how such a system learns to discriminate

(a) x from y if only the two patterns are given.
(b) x from other patterns.
(c) A class of x patterns from a class of y patterns.

Let there be n A-cells and the signal sent from the r^{th} A-cell to D_x be γ_{rx}. Then the total signal at D_x *is* $\epsilon X_{r\gamma x}$ where X_r is 1 or 0 according as A_r is connected or not to D_x; and D_x fires if $\epsilon X_{r\gamma rx} - T > 0$ where T is the threshold of D_x. The equation $\epsilon X_{r\gamma rx} - T = 0$ is that of a plane π in n-dimensional A space. The pattern x at S will cause activity at A which corresponds to a point P_x in the A space; pattern y corresponds to a point P_y.

Variation in the values of γ will cause the position of the plane π to change. The reward rules can be made such that P_x and P_y lie on opposite sides of the plane π; this is shown for two dimensions of A-space in Fig. 12a.

Clearly a much difficult task would be to adjust the plane π so that P_x lay on one side and all the $(2^n - 1)$ other possible patterns lay on the other side; it could even be impossible as in Fig. 12b.

However, the pattern P_x could be separated from all other P if an extra A-dimension were introduced and defined so that P_x lay above the plane of the paper and all other P below.

Many variations of the reward rules have been considered; it is essential that they cause the π plane to converge towards a limiting position. The rate of convergence may be called a rate of learning but this is a less important matter than the question of whether a π plane could even exist which would completely separate a *class of* x patterns from a *class of* y patterns. Rosenblatt suggested in early work that such a plane could always be found by the machine. In general, this is not so. In figure 12c, it can be seen that the conditions for separating all P_x from all P_y by a plane are much more limited than in the case of Fig. 12b. Again, the creation of a new A-dimension may make it possible. This is what happens when a symbol is introduced; in an arbitrary way all P_x can be given the value 1 and all P_y the value 0 for a dimension normal to the plane of the paper.

Alternatively a new or different A-dimension can be created by changing connexions from the receptors S to the A-cells. Selfridge has emphasized that it matters very much how connexions are made from the S to the A layer; he demands that these connexions be plastic, just like the connexions from A to D. Taking a leaf out of the book on Evolution Theory, he introduces two important principles for modifying the connexions from S to A:

(1) If an A_r cell contributes to a fairly accurate decision D_x (i.e. if γ_{rx} becomes large) but not to an always correct decision, then minor random changes are made in its connective system. (Mutations)

(2) If two such A cells so contribute they are combined in a single cell with all the connexions of both. (Conjunction).

These systems demand an independent variable conductance between each A-D connexion. If there are r A-cells and x D-cells there must be $(r \times x)$ variables. They also demand that all paths to D_x be modifiable by T_x, and similarly for all

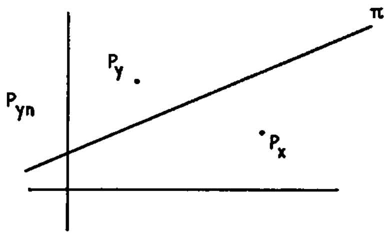

Fig. 12a

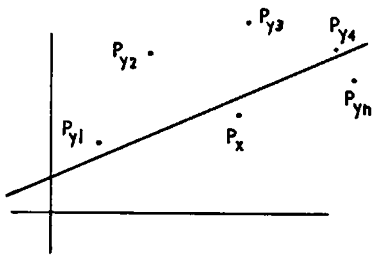

Fig. 12b

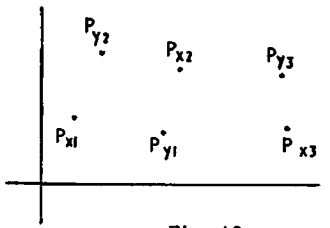

Fig. 12c

FIGURE 12a, b, c Increasing difficulty in conditions for the existence of a plane π to separate sets of points. The two-dimensional diagram refers to n-dimensional A-space.

other D. An idea which has not yet been fully examined is to incorporate Uttley's two variable theory. Each A cell would send out a larger signal after each occurrence of the corresponding S pattern. Each D_x-cell would become less sensitive each time its output had agreed with that of the corresponding teacher T_x. There would then be only $(r + x)$ variables and the total system of connexions would be simpler.

SUPPORTING BIOLOGICAL WORK

Since, on the whole, theories of plastic networks have been devised to simulate certain forms of animal behaviour these theories cannot be tested by means of psychological data. One must look to physiology for confirmation.

Recoding to reduce redundancy

A good example of this occurs in the retina of limulus (Hartline, 1938) and frog (Barlow, 1953) and cat (Kuffler, 1953). The image on the retina will, in general, consist of patches of fairly constant illumination. It is only the changes in illumination which convey information; only these need be transmitted. If one places a microelectrode on the retinal surface and explores with a small light spot, one finds a position of maximum sensitivity surrounded by a circular annulus which is inhibitory.

If the total area under this curve is zero the effect of uniform illumination on the receptor cell will also be zero. The coding introduced by the "lateral inhibition" is that of taking the Laplace Transform $\partial^2 I/\partial_x{}^2 + \partial^2 I/\partial_y{}^2$ of the illumination I. As a result, only information about contours is passed, namely, that of their brightness difference and curvature: information in a single optic fibre about the direction of contours is lost in this transformation. However, Hubel and Wiesel (1959) have found that at the visual cortex the coding has become more subtle; the circular inhibitory zone has been lost in favour of the patterns of figure

Consider only the unit of Fig. 13b and the effect on it of lines of different length and direction. The maximal excitation will occur from a patch of light the same shape as the excitatory area. Lines in different directions will have less effect; a line at right angles to the patch will have zero effect. It follows that information at a point on the cortex is about a corresponding point on the retina AND on the state of its neighbours. Hubel's cells give information as to the direction of contours passing through the corresponding point on the retina. Here we recall Selfridge's statement that it matters very much how receptor units S are connected to association units A (Fig. 11). The system described above is suited to a visual environment containing contours as a frequent feature. It may have evolved or it may have adapted during life. To resolve this point Hubel's work should be repeated on a range of kittens reared in a featureless visual field.

Lettvin, Maturana and Pitts (1959) have found, for the frog, that different forms

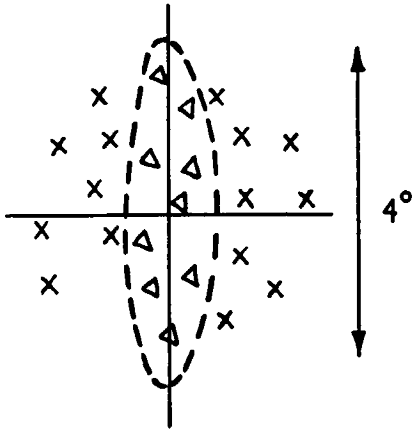

Fig. 13a

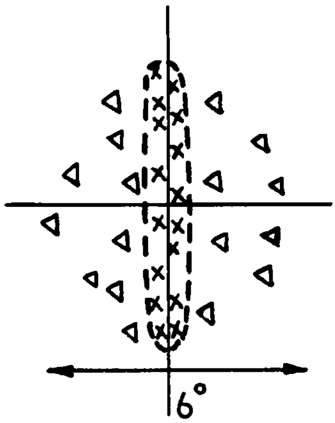

Fig. 13b

FIGURE 13a, b Responses of cell in the cats striate cortex to a 1° spot of light. *x*, areas giving excitation; Δ, areas giving inhibitory effects. (After Hubel and Wiesel).

of coding exist at different depths in the tectum. For example, at a particular level, cells become active only for moving contours. Here, the experimental work of Hassenstein (loc. cit.) and the theories of Reichardt (loc. cit.) are highly suggestive. A network such as that of Fig. 8 would give rise to the phenomena described by Lettvin et al.

The transformation of signals in auditory pathways have been exhaustively studied by Rosenblith and co-workers (1959) particularly from click stimuli. Similar work has been carried out on visual pathways in monkey (Gutierrez and Berger, 1959). Powerful research tools have been developed for analysing large samples of impulse trains which study any nerve pathways (Barlow, 1961). Special auto-correlation and cross-correlation computers have been built as well as a very useful "Average Response Computer" (Clark, 1958).

Facilitation, adaptation and potentiation

The idea of facilitation is an old one. Association can be built between two novel stimuli apparently without limit. If a novel stimulus can gradually arouse a novel response some new pathway must have been formed. To test this theory physiologically (Burns, 1961) implanted a microelectrode in the cortex of a cerveau isolee in cat. He found a pattern of random firing whose mean rate could be altered if a d.c. potential was applied to the electrode. Furthermore, if the mean rate was thus artificially raised for about a minute, the subsequent mean rate was lowered considerably, and although it increased slightly, it rose to a steady new level which was much lower than its value before the d.c. bias was applied. The cell had become permanently reduced in sensitivity. The length of the experiment was about an hour. The effect was reversed if the d.c. bias was such as to decrease firing rate; this finding conflicts with the hypothesis of facilitation. However, this property of adaptation, i.e., increased threshold, is required by Uttley's Conditional Probability Theory. Uttley's related prediction is that, after a period of increased firing a cell should have a greater effect on those to which it transmitted impulses; this property, post-tetanic potentiation, has been reported in spiral neurons (Eccles, 1953), and also been seen in preliminary experiments on cortex (Burns, 1961).

CONCLUSIONS

Non-plastic networks

1. From the theory of the logical design of computers it is possible to construct networks such that specific input patterns of signals give rise to specific output patterns.
2. Such networks must contain classification systems for analysing input patterns and synthesizing output patterns.
3. A complete classification system for n inputs would require 2^n indicating units, and this is not practicable in a system with more than a few inputs. Adaptive classification is therefore essential.
4. If there is redundancy in input signals of a form which is always present in the external environment of a classification system, then some preliminary coding of a fixed nature is of great advantage. Two examples have been given:

    (a) Objects important to an animals survival are, in general, bounded by *surfaces* which, projected onto a retina give rise to *contours*. Contour detectors can be devised by means of logical circuits. Such principles are found in retinae, but it is not yet known whether they are inherited or are developed plastically in early life, as a result of experiencing this form of redundancy.

    (b) The detection of *movement* is important and, again, it can be effected by inherited logical circuits (Reichardt loc. cit.) or it can develop plastically (Uttley loc. cit.).

Plasticity

5. Plastic coding devices have been made which can transform input signals into less redundant less frequent signals.
6. Lattices of units have been constructed which compute the conditional probability of one pattern (set of input signals) given that any other pattern is occurring. For complete discrimination of all patterns such a system must have 2^n units if there are n input channels.
7. Plastic classification systems have been designed which will learn to discrimi-

nate as many of the most frequent input patterns as there are units in the system. The required laws of plastic interconnexion are different for different workers.

Beurle demands increased sensitivity in the receiving unit after becoming active.

Selfridge, Minsky, Rosenblatt and Taylor demand facilitation between units.

Uttley's system demands two changes in the state of a unit after becoming active: (a) increased effect of output signals; (b) decreased sensitivity.

8. A class of signal patterns can be discriminated from patterns of another class if some particular signal occurs with most members of the class. This signal, by labelling members, acts as a symbol for the class; plastic networks have been devised which will compute the probability that the symbol should be attached to a future unmarked pattern. An essential property of such networks is that they shall try different combinations of the input signals, in order to discover which of them correlates most highly with the symbol.

Physiology

Contact between mathematical theory and biology have been made at a few points. At other points the gap can be seen to be narrowing.

9. Transformations of nerve signals between different areas of a nervous system have been observed which can be explained in terms of logical circuits. They all reduce redundancy of the signals in pathways.

10. Regarding variability of connexions between cortical neurons, the most recent evidence is against increased facilitation with use and against increased sensitivity to received signals. Cortical neurons appear to adapt and to become less sensitive with use. Preliminary experiments also suggest that there may be post-tetanic potentiation in cortical synapses.

REFERENCES

ALLANSON, J. T. 1956. The reliability of neurons. First International Congress on Cybernetics. Gauthier-Villars. Paris.

BARLOW, H. B. 1953. Summation and inhibition in the frogs retina. J. Physiol., **119**, 69–88.

BARLOW, H. B., and DONALDSON, P. E. K. 1958. Sensory mechanisms, the reduction of redundancy, and intelligence. Proc. NPL Symp. No. 10, Mechanisation of Thought Processes, HMSO, 1959, **2**, 535–557.

BEURLE, R. L. 1956. Properties of cells capable of regenerating pulses. Phil. Trans. Roy. Soc. B. **240**, 55–94.

BURNS, B. DE L. 1961. Private communication.

CLARK, W. April 1958. Quarterly Progress Report. Radiation Laboratory of Electronics, M.I.T.

GRAFSTEIN, B., BURNS, B. D., and HERON, W. 1959. Activity of cortical neurons in response to patterned visual stimuli. Procs. of the Second International Meeting of Neurobiologists, Amsterdam. Elsevier Publishing Company, Amsterdam, 1960.

GUTIERREZ, O. C., and BERGER, E. April 1959. Quarterly Progress Report 53. Radiation Laboratory of Electronics, M.I.T.

HARTLINE, H. K. 1938. The response of single optic nerve fibres of the vertebrate eye to illumination of the retina. Amer. J. Physiol., **121**, 400–415.

HASSENSTEIN, B., and REICHARDT, W. 1956. First International Congress on Cybernetics. Gauthier-Villars, Paris.

HUBEL, D. H., and WIESEL, T. N. 1959. Receptive fields of single neurones in the cat's striate cortex. J. Physiol., **148**, 574–591.

KUFFLER, S. W. 1953. Discharge patterns and functional organization of mammalian retina. J. Neurophysiol., **16**, 37-68.

LETTVIN, J. Y., MATURANA, H. R. and PITTS, W. H. 1959. What the frog's eye tells the frog's brain. Proc. I.R.E., **47**, 11, 1940–1951.

MINSKY, M. L. 1958. Some methods of artificial intelligence and heuristic programming. Procs. NPL Symp. No. 10, The Mechanisation of Thought Processes, HMSO, 1959, **1**, 3.

MCCULLOCH, W. S. and PITTS, W. 1943. A logical calculus of the ideas immanent in nervous activity. Bull. Maths. and Biophysics 1943, **5**, 115.

NEUMANN, J. VON. 1945. Report on EDVAC. Moore School of Electrical Engineering, University of Pennsylvania, Philadelphia, Penn.

NEUMANN, J. VON. 1956. Probabilistic logics and the synthesis of reliable organisms from unreliable components. Automata Studies, edited by C. E. Shannon and J. McCarthy. Princeton University Press, Princeton, N. J.

PAPERT, S. 1960. Redundancy and linear logical nets. Bionics Symposium. Dayton, Ohio. Published by Office of Technical Services, U. S. Department of Commerce, Washington 25, D. C. U.S.A.

ROSENBLITH, W. A. 1959. Sensory Performance of Organisms. Rev. Mod. Phys. **31**, 2, 532–545.

ROSENBLATT, F. 1958. Two theorems of statistical separability in the perceptron. Procs. NPL Symp. No. 10, Mechanisation of Thought Processes, HMSO, 1959, **1**, 419.

SELFRIDGE, O. G. 1958. Pandemonium: a paradigm for learning. Procs. NPL Symp. No. 10, Mechanisation of Thought Processes, HMSO, 1959, **1**, 511.

SHOLL, D. A., 1955. The organization of the visual cortex in the cat. J. Anat., **89**, Pt. 1.

TINBERGEN, N. 1951. The study of instinct. Clarendon Press, Oxford.

TURING, A. M. 1937. On computable numbers. Proc. London Math. Soc., Ser. 2, Vol. 42, 230–246.

UTTLEY, A. M. 1954. The classification of signals in the nervous system. E.E.G. Clin. Neurophysiol., **6**, 479.

UTTLEY, A. M. 1956a. Conditional probability machines and conditioned reflexes. Ann. Math. Studies, edited by C. E. Shannon and J. McCarthy. No. 34, Princeton University Press, Princeton, N. J.

UTTLEY, A. M. 1956b. A theory of the mechanisms of learning based on the computation of conditional probabilities. Procs. of the First International Congress on Cybernetics, Namur, 1956, Gauthier-Villars, Paris.

UTTLEY, A. M. 1958. Conditional probability computing in a nervous system: Procs. NPL Symp. No. 10, Mechanisation of Thought Processes, HMSO, 1959, p. 119.

WALTER, W. G. 1951. Les machines a calculer et la pensee humaine. Colloq. intern. Centre natl. recherche sci. Paris, **12**, 407–421.

BARLOW, J. S. April 1961. A versatile analog computer for neurophysiological research. Quarterly Progress Report No. 61. Radiation Laboratory of Electronics, M.I.T.

ECCLES, J. C. 1953. The neurophysiological basis of mind. The principles of neurophysiology. Clarendon Press, Oxford, p. 194–206.