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PAPER 4-1

SENSORY MECHANISMS, THE REDUCTION OF REDUNDANCY, AND INTELLIGENCE

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by

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4-1. SENSORY MECHANISMS, THE REDUCTION OF REDUNDANCY, AND INTELLIGENCE

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SUMMARY

PSYCHO-PHYSICAL and physiological investigations have shown that the eye and the ear are remarkably efficient instruments: consequently the amount of information being fed into the central nervous system must be enormous. After a delay, which may vary from about 100 msec. to about 100 years, this information plays a part in determining the actions of an individual: therefore some of the incoming information is stored for long periods.

The argument is put forward that the storage and utilization of this enormous sensory inflow would be made easier if the redundancy of the incoming messages was reduced. Some physiological mechanisms which would start to do this are already known, but these appear to have arisen by evolutionary adaptation of the organism to types of redundancy which are always present in the environment of the species. Much of the sensory input is not shared by all individuals of a species (eg. stimuli provided by parents, language, and geographical locality) so a device for "learning" to reduce redundancy is required. Psychological experiments give indications of such mechanisms operating at low levels in sensory pathways, and "intelligence" may involve the capacity to do the same at high levels.

In order to exemplify the operations contemplated, a device which reduces the correlated activity of a pair of binary channels is described.

THE usual mechanistic approach to the higher nervous system begins with a consideration of the factors which can be shown to have an immediate effect on the output of the nervous system. The commonest starting point is the simple monosynaptic reflex in which a single sensory input controls a single motor output, as shown diagrammatically in *fig. 1(a)*. The next stage is to elaborate this by taking into account other sensory modalities, inhibition, internuncial neurones, and controlling neurones from elsewhere

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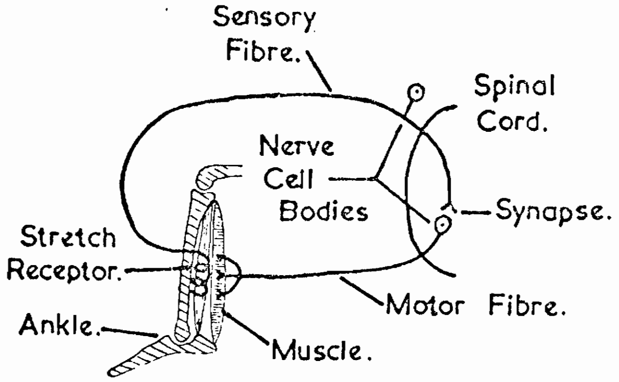

Fig. 1(a)

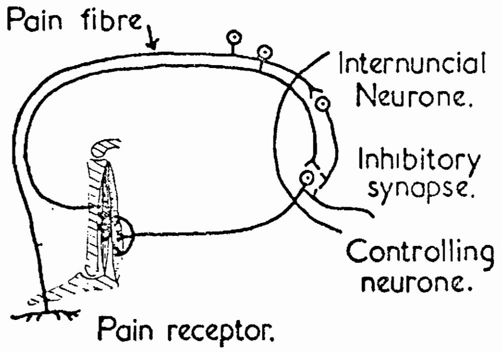

Fig. 1(b)

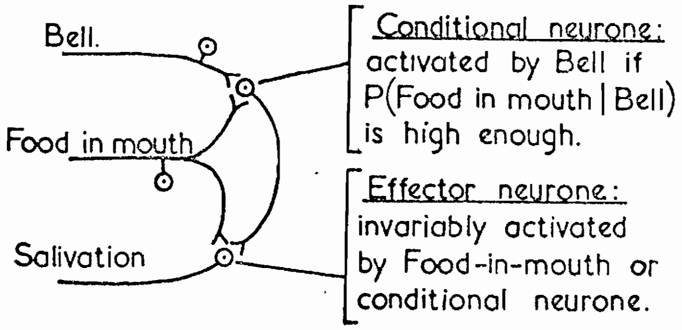

Fig. 1(c)

Fig. 1. Diagram showing approach to higher nervous function from motor (effector) side. (a) monosynaptic stretch reflex; (b) same with addition of internuncial neurones, controlling neurones from other parts of the central nervous system, and inhibition by pain endings; (c) conditioned reflex.

in the nervous system, as shown in *fig. 1(b)*. With all its trimmings this gets one to a stage of complexity perhaps comparable to that of an automatic tracking radar set, or the automatic pilot of an aeroplane. It will show none of the plasticity or adaptability to new surroundings which is characteristic of the higher nervous system, so the Pavlovian conditioned reflex is next introduced. The principle here is that if there are two sensory stimuli (Bell and food in mouth), one of which (food in mouth) always produces a response (salivation), then if they occur jointly with sufficient frequency, the one which, to begin with, did not cause a response, begins to do so (Bell alone causes salivation). This is shown diagrammatically in *fig. 1(c)*, and is perhaps the simplest type of learning behaviour that has been studied in animals, though it has not been investigated in a simple isolated preparation as the diagram might suggest. Uttley (1954, *refs. 22 and 23*) has clarified the principles of operation of such mechanisms and built conditional probability devices which show the same properties of learning and inference.

Now the simple feedback diagram in *fig. 1(a)* has a single input channel, *fig. 1(b)* and *(c)* have two inputs, and Uttley's machine has up to five inputs; but a human brain has something like 3×10^6 sensory nerve fibres leading into it. If it could be supposed that a million or so devices like that of *fig. 1(c)* would deal with the sensory inflow one would be well satisfied with the understanding gained from this approach: but this is not so. The essential operation in a conditional probability device is to measure the frequency of occurrence of *combinations* of activity in the input. Now if the number of binary inputs is increased from two to a million the number of possible combinations is increased from 2^2 to $2^{(\text{million})}$; an arrangement like that of *fig. 1(c)* takes one less far than at first sight appears. I think it follows from this consideration that conditional probability machines cannot be fed with raw sensory information, and the problem of digesting or processing the sensory information entering the brain is an important one. Furthermore, modern electrophysiological techniques are making it possible to record from nerve cells at various levels in the sensory pathways, so this is a problem which is becoming accessible to experimental investigation.

In this paper I have first tried to make rough estimates of the rate at which information flows into the human brain. It is then suggested that an essential step in organising this vast inflow is to derive signals of high relative entropy from the highly redundant sensory messages. For this something similar to the optimal codes discussed by Shannon (1949, *ref. 19*) needs to be devised for the sensory input, and the steps required to do this are considered. Finally, a modified form of such recoding is proposed, some evidence that it occurs is brought forward, and it is suggested that the idea may be extended to cover some of the processes going on in consciousness and called reasoning or intelligence.

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1. THE SENSORY INFLOW

(a) Properties of Nerve Fibres

We are equipped with sensory instruments of astonishing sensitivity and versatility which supply information about the environment to the central nervous system. This information is carried along nerve fibres, and since a good deal is known about what these fibres can and cannot do, one can derive an approximate upper limit to the rate at which information enters the brain. If the simple assumptions are made that (i) the maximum frequency of impulses is 700/sec, and (ii) in 1/700th.sec a nerve can only be used to indicate the presence or absence of an impulse, then the maximum rate at which it can transmit information is 700 bits/sec. Mackay and McCulloch (1952, *ref. 16*) point out that the nerve might be used more efficiently if, instead of detecting the presence or absence of an impulse, the intervals between impulses are used to convey information. Using such pulse interval modulation, and assuming (i) accuracy of estimation of intervals of 0.05 msec, (ii) a minimum interval of 1 msec, they give the maximum capacity as 2880 bits/sec. This would require a mean frequency of 670 impulses/sec, but at a mean frequency of 50/sec, such pulse interval modulation still allows 500 bits/sec to be transmitted. These figures are actually too low, because Mackay and McCulloch incorrectly assumed that the optimum distribution of intervals was uniform instead of exponential: however, if the other assumptions are granted, they show clearly that a single nerve fibre could be used to transmit information at a rate well above 1000 bits/sec.

The total capacity of the sensory inflow appears to be above 3×10^9 bits/sec, but it is certain that nothing like the full capacity is utilised. The mean frequency of impulses must be far below the optimum; peripheral nerves appear to use pulse frequency rather than pulse interval modulation, so that there will be high serial correlations between the values of intervals; furthermore, there are generally considerable overlaps in the pick-up areas of neighbouring fibres, which are therefore bound to show correlated activity. Finally, the figure for the performance of a nerve fibre given above might be approximately true for the large diameter fibres, but those of smaller diameter, which make up a large fraction of the total number, must have a smaller capacity. It would be pure guesswork to try to allow for these factors, but one can get indications of the utilised capacity from two other sources.

(b) Sensory Ability

Jacobson (1950, 1951 *refs. 13,14*) has made estimates of the informational capacity of the ear and the eye. For the ear he calculated 50,000 bits/sec from the number of discriminable pitches (about 1450), the number of discriminable intensities at each pitch (average about 230), and the time required

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to make such discriminations (1/4 sec). This does not make any allowance for masking - the observed fact that the presence of one tone interferes with the perception of other tones. Jacobson calculated that this would reduce the information capacity by a factor of about six, bringing it down to 8,000 bits/sec. Now there are 30,000 nerve fibres from the ear, so each fibre must carry an average of about 0.3 bits per sec.

For the eye he calculated from published data of central and peripheral acuity that there were 240,000 resolvable elements in the visual field (he seems to omit a factor of two in the integration, but this is perhaps compensated by the rather high figure for acuity which he uses). He supposes that each element can be discriminated at two intensities, with an average temporal resolution of 1/18 sec. These figures give 4.3×10^6 bits/sec. In the optic nerve there are just under a million fibres, so about 5 bits/sec are conveyed on the average by each fibre,

These are crude estimates. For instance, no account has been taken of colour discrimination, or of the ability to localise a sound by binaural effect and judge depth by stereoscopic vision. Nevertheless, they are probably of the right order of magnitude and they are probably good enough to justify the claim that optic nerve fibres carry much more information than those of the auditory nerve. This may be significant and will be referred to later.

These figures suggest that total sensory inflow along the three million sensory fibres is rather under 10^7 bits/sec.

(c) Communication bandwidths

The capacity of the communication channels engineers need to transmit auditory and visual signals is clearly related to the capacity of the sensory pathways. Engineers, in the interests of economy, may be expected to try to use the narrowest bandwidths which will satisfactorily load up the sense organs involved, and recipients may be expected to insist that such satisfactory loading is not too far short of normal loading.

Ten k.c. bandwidth at 40 d.b. signal noise ratio give a good quality auditory signal, and has a capacity of 133,000 bits/sec. This is more than ten times Jacobson's final figure for the capacity of the ear (8,000 bits/sec), and the discrepancy is presumably due to (i) the transmission of relative phases of the frequency components, which gives information not utilised by the ear - at least in the type of discrimination taken account of by Jacobson; (ii) the failure of the engineer to exploit the loss of efficiency of the ear which results from masking.

A satisfactory 400 line television picture requires three megacycle bandwidth at about 10 d.b. signal-noise ratio, and this corresponds to 1.2×10^7 bits/sec. One is much more aware that such a television picture falls short of one's normal visual signals than one is in the case of a

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10 k.c. 40 d.b. auditory signal because it does not fill the visual field, and lacks detail and colour, but it is still more than double Jacobson's estimate of the eye's capacity. In this case the most notable matching errors are the failure to exploit (i) low peripheral acuity of the eye, (ii) reduced temporal and spatial resolving power in low intensity regions of the image.

Engineers seem to require 5 - 10 bits/sec channel capacity per nerve fibre to load up our sensory pathways, but the discrepancies between this figure and those obtained from direct estimates of sensory abilities can probably be attributed to poor matching.

(d) *Time of storage*

Not only is the input to the nervous system enormous, but some, at least, of the messages received are stored for very long periods. Most people would agree that sensory impressions can be recalled after a lapse of, say, 70 years, and sometimes a person can produce objective evidence of the accuracy of his recollections. In addition there are, of course, many sensory impressions which cannot be recalled, but which have, none the less, left their mark: we do not remember the successes and failures by which we acquired the correct usage of 'yes' and 'no', but this correct usage is often retained beyond the retiring age. If one allows for fifty years of waking life, the total sensory input is something like 10^{16} bits. Complete storage of all this information is neither likely to be possible nor, of course, is it what is needed.

(e) *Fate of Sensory Information*

The rest of this paper is about a suggested plan of storing and displaying this enormous sensory input, but one must first have some idea of the use that is made of the sensory information and the neural equipment which is available for dealing with it. According to Craik (1942, *ref.4*) the sensory information is used to build up a model of the external world which provides a basis for determining what course of action is most likely to lead to the survival of the individual and his species. That is a brief answer to the first question, and it also gives the answer to another fact which might otherwise be puzzling. A man can only make decisions on the basis of sensory information at a maximum rate of about 5 to 25 bits/sec. (Hick, 1952, *ref.11* Quastel, 1956, *ref.18*): why, then, does he need a sensory input of 10^7 bits/sec.? Craik's answer would probably have been that the greater the sensory input the more complete and accurate the model, and hence the surer its basis for planning survival.

The question of the equipment available can also, because of our ignorrance, be answered briefly. There are some 10^{10} interconnecting nerve cells in the central nervous system, and quite a large proportion of them must be

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available for the task of dealing with the sensory input and building up the model. We are only beginning to determine the properties of these cells; it has been known that their long processes transmit information as all-or-none impulses for more than fifty years, but how information is stored is not yet understood. In what follows I shall be talking about *what* the nervous system does rather than *how* it does it, so our ignorance of the method of storage of information is not too serious. The problem might be discussed abstractly, but for the sake of a definite model one can think of each nerve cell having "excitation laws" which determine the conditions under which it becomes active, and suppose that these laws can be changed so that it becomes active in response to a different set of patterns of activity in the nerve cells in contact with it. The excitation laws for all the neurones would then form a store of information and the current display would consist of the pattern of nerve cells which are actually transmitting impulses down their long processes at any given moment.

With this model in mind the problem is: what should the excitation laws of the neurones be, and how should they be alterable, in order that the display of activity shall help the individual and species to survive in the situation giving rise to the current sensory input? To avoid basing the argument on uncertain preconceptions of what the brain does, one could put it in more general terms in this way. The barrage of nervous impluses reaching the nervous system seems to be unmanageably large; how should a selection of this activity be made for current display and future reference?

2. ORGANISATION OF THE SENSORY INPUT

The proposition is that the initial selection is performed according to those statistical properties of the past sensory messages which determine how much information particular impulses convey. It is supposed that the sensory messages are submitted to a succession of re-coding operations which result in reduction of redundancy and increase of relative entropy of the messages which get through. Ideally one might imagine that an optimal code is constructed, so that the output, or "display" of current input, has no redundancy, relative entropy 1, and carries all the information of the input. This ideal obviously cannot be reached, but the re-coding operations are supposed to tend towards the ideal: that is, outputs are derived from the input, which have high relative entropy and carry as much of its information as possible.

Shannon has shown that it is possible in principle to obtain near optimal coding if a sufficient number of messages of a given length have occurred to give knowledge of the statistical structure of the messages, and if delays are permitted between input and output. Fano and Huffman (1953, *ref. 12*) have described procedures for constructing such codes. The first steps are to define what shall constitute a single message and then to measure the frequency of occurrence of all possible messages of this class. Clearly the class cannot be the whole of the sensory input to the brain up to a particular moment, for this message has only occurred once. The input must be sub-divided in time, and first consider the operation required to re-code messages of duration, say, one second. The capacity of the input channel has been shown to be about 3×10^9 bits/sec. which corresponds to $10^{(\text{thousand million})}$ possible messages per second. If one takes account of the restrictions which reduce the utilised capacity to some 10^7 bits/sec., and considers messages of one-tenth second duration, there are still some $10^{300,000}$ possible messages. It would clearly be hopeless to devote neural equipment to the counting of each possible message, for it is highly improbable that any single message will be exactly repeated and most of such equipment would be unused at death. This is, essentially, the same difficulty that was levelled against the idea that conditional probability devices could be served with unprocessed sensory data, but when one considers optimal coding there is a possible solution. Because the code is reversible, no information is lost by re-coding small sections of the sensory input independently, and such preliminary re-coding will enable the whole message to be passed down a channel of smaller capacity, and thus facilitate subsequent steps.

The idea is best illustrated by considering the order in which different types of redundancy might be encountered, and eliminated, during the successive re-coding operations. First there is the very large amount which results from the inefficient utilisation of peripheral nerve fibres. Looking only at the nerve impulses as they arrive, it would be found that impulses occurred at different mean rates in different fibres and in all of them at rates well below the optimal frequency for information transmission. This type of inefficient utilisation of a set of communication channels is a form of redundancy, but for reasons discussed later (Section 4) it may be less important to eliminate than other forms: for the moment one can consider the capacity of a nerve fibre as determined, not by maximum frequency of impulses, but by the mean frequency at which they occur.

Next, still looking only at the impulses as they reach the central nervous system, it would be found that impulses do not occur completely at random in time but tend to follow one another in sequences and bursts: the first re-coding operation might be a mechanism which reduced the serial correlations so that the same amount of information was carried by fewer impulses. In addition it would be found that certain groups of nerve fibres tended to become active at the same time. These would be fibres whose receptive fields on the sensory surface overlapped, so that this particular form of redundancy results from the anatomical properties of fibres and sense organs, just as the serial correlations in time result from the fact the intensity of a stimulus is coded as frequency of impulses at the sense organs.

These first steps, then, would reduce the orderliness in the sensory messages which results from characteristics of the sensory apparatus. But if this orderliness can be eliminated, so can that resulting from the characteristics of the environment which is providing these stimuli. For instance, it will often happen that a stimulus covers more than a single point on the sensory surface and therefore causes activity in a group of fibres larger than those whose receptive fields overlap. Advantage could be taken of this to reduce the number of impulses required to convey information about such a stimulus. Again, a stimulus will often be moved across a sensory surface causing excitation in sequences of nerve fibres. Such repeated, ordered, sequences of activity would be a form of redundancy which could be reduced by suitable re-coding. In fact, any pattern of stimuli which represents a departure from complete randomness - such as simultaneous stimuli at different points on the sensory surface, stimuli which are maintained for long duration of time, ordered sequences or cycles of stimuli - present an opportunity of reducing the magnitude of the sensory inflow by suitable re-coding. It is clear that many of the complex features of our environment will come into this category. For instance, the stimuli which result from an animal's parents or its habitat are repeated frequently, and economies could be effected by reducing the space in the sensory representation occupied by these familiar stimuli and allowing more space for the infrequent and unexpected stimuli.

It is suggested, then, that the processing or organisation of sensory messages is carried out by devising a succession of optimal or near-optimal codes adapted to the messages which have been received. In the early stages the total inflow will be sub-divided into many small sections, presumably taking in each section the messages coming along neighbouring fibres during a short interval of time. In the later stages the coded outputs will be re-mixed, possibly with the addition of delayed inputs (as utilised by Uttley in conditional probability devices) to allow detection of movement and other ordered sequences of activity, and then will be sub-divided again into small sections. Thus in the later stages the nerve messages being re-coded may be derived from more and more remote parts of the sensory inflow and may also come from sensory stimuli more and more separated from each other in time of occurrence. It will be seen that at each stage storage of some of the sensory information is required in order to construct the optimal code, and thus the code itself forms a kind of memory.

Now the idea that our brains detect order in the environment is not new. Empiricist philosophers have talked of percepts being associated sense impressions, and of causality corresponding to invariant succession of sense impressions. Behaviourists have emphasised the importance of association, and Gestalt psychologists talk of ordering sensation according to certain schemata (though here there seems to be some confusion as to whether the ordered schemata are derived from sensations or imposed upon them). Thus the fact that our higher centres are much concerned with the redundancy of the sensory messages has often been pointed out, but two aspects of this fact have not, I think, been so widely recognized. First, the detection of redundancy enables the sensory messages to be represented or displayed in a more compact form; and second, the reduction of redundancy is a task which can be subdivided and performed in stages. *Figure 2* shows diagrammatically how the suggested scheme of storage and display compares with more othodox representations of memory and consciousness. It will be seen that in the present scheme a large part of the storage of information occurs before the display - that is before the level of re-coding which might correspond to conscious awareness of sensory stimuli. The re-coding is supposed to continue at conscious levels, so some of the information reaching consciousness is also stored, but this would only be sufficient, first, to enable the process of building up the code to continue, and second to enable "useful" association to be made between motor acts and features of the current sensory input (e.g. between salivation and bell).

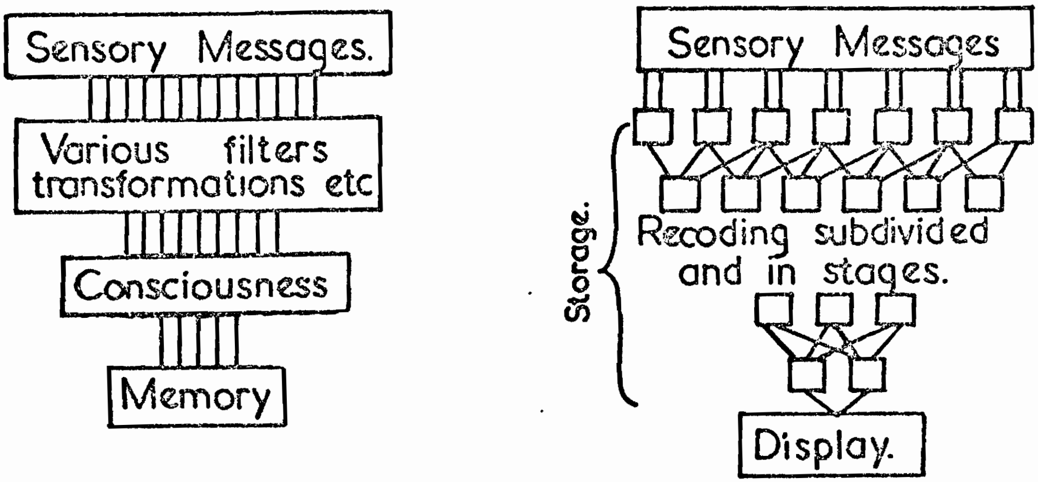

Fig. 2. Diagram contrasting memory *after* consciousness in orthodox scheme with storage *before* display in optimal coding scheme.

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It seems a help to consider the processing of sensory information as optimal or near-optimal coding for two reasons. Practically, it enables the subject to be approached along the firm path of sensory physiology instead of through the shifting sands of conscious introspection and philosophy. And conceptually it shows a way in which complete mental acts, which seem appalling in their complication and perfection, may be sub-divided into a succession of much simpler operations; this is clearly a prerequisite for gaining an understanding of the physiological basis of mental function.

It is worth noting that the possibility of sub-division rests on Shannon's proof of the possibility of near-optimal coding; if the early transformations of the sensory information were not reversible, redundant features which are detected later might be lost: and if the earlier transformations did not increase the relative entropy of the messages, they would not facilitate the detection of higher order redundancy.

3. DESIRABILITY OF OPTIMAL CODING

In the last section an outline scheme for dealing with the enormous sensory inflow was suggested. In this section some reasons for the desirability of optimal coding are put forward. It will be argued that it is desirable on the grounds of accessibility, stability, and economy, and because it requires storage of information sufficient to form a model of the animal's environment. Of course, such arguments for its desirability are not sufficient reasons for believing that it actually occurs.

(a) Accessibility.

Optimal coding will improve the accessibility of information in two ways. First, the capacity of the display required for the current sensory input will be decreased. This simplifies the task of finding useful associations just as reducing the size of a haystack simplifies the task of finding needles. The second way is less obvious. In messages of high relative entropy, the probability of a given message occurring is close to the product of the probabilities of the individual signs which make it up. Now a dog feeds once or twice a day, and when looking for sensory correlates of salivation it would not be worthwhile to search among combinations of individual signs whose probability of joint occurrence was so low that they would be expected only, say, once a week, nor amongst those whose probability was so high that they would be expected, say, once an hour. If the input to a conditional probability device is known to be of high relative entropy, great economies of design are possible.

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(b) Stability

It is sometimes argued that redundancy is a good thing because it protects a message from noise. There may well be random effects inside the nervous system against which the storage and display of sensory information needs protection, but the redundancy of the internal representation which would achieve this is not in general the same as the redundancy which occurs in the sensory input. When driving at night the internal representation of a pedestrian crossing the road requires as much protection as the representation of the blinding glare from an oncoming car, but in the incoming sensory message the former may be represented by a barely significant disturbance in the pattern of nerve impulses, the latter by high frequency volleys of impulses in many fibres. Stability of storage and display require, at least, a re-adjustment of the redundancy of the sensory messages.

(c) Economy in transmission and storage.

Sensory information has to be transmitted from place to place in the central nervous system and the reduction of redundancy before this is done would enable the number of internal connecting fibres to be reduced. An example where the economy so effected seems to be particularly desirable is the connection between the eye and the brain. It would clearly interfere with the mobility of the eye if the optic nerve was very much larger than it is, and according to Jacobsen's estimates it would have to be fifteen times larger if the nerve fibres were utilised as inefficiently as they are in the ear. The attainment of this 15-fold economy may, as Jacobsen suggests, be the main function of the nervous layer of the retina which links receptors to optic nerve fibres. Squids and octopuses form an interesting comparison, for they have eyes which are comparable optically to those of vertebrates, but their retina is much simpler with no synaptic layer - the optic nerve comes direct from the receptor cells. It is bulky, containing a vast number of fibres, and seems likely to be a factor restricting the mobility of their eyes.

The same argument might be applied to storage of information, since it is clearly more economical to store messages after their redundancy has been reduced. Here, however, there is a complication. The devising of a redundancy-reducing code requires storage of certain properties of the sensory message, and it has not been shown that more capacity would be saved by storing messages after re-coding than would be utilised in devising the code. The condition that this should be so depends upon the number of the times that the code, once devised, is subsequently utilised, but a discussion of this point cannot go far without knowing what parts of the sensory inflow are in fact stored: the argument of the next section is that the coder itself stores sufficient information to form a working model of the animal's environment, and therefore represents a large fraction of the total storage the animal needs.

(d) Modelling the Environment.

Craik suggested that sensory information was used to form a model of the animal's environment. By a model one does not mean a simple copy of those aspects of it which have given rise to sensory stimuli: it must also mimic the structure of the environment, so that an operation performed on the model will give the same result as the analogous operation performed on the environment. When the schoolboy turns his model engine round, he receives visual stimuli similar to those he would have received if a real engine had been turned round in front of him. The model imposes restrictions on the sensory stimuli which are received in certain situations, these restrictions being the same as those inherent in the properties of the object modelled. Now it is precisely these restrictions - the departures from complete randomness of the sensory input - which the coder utilises to increase the relative entropy of the signals. The particular code adopted is related to the particular restrictions of past sensory inputs and is therefore, in a sense, a model of the animal's environment. In the example above, the model was static, but the restrictions must often be dynamic; sets of sensory stimuli frequently follow one another in a repeated sequence, and such repeated sequences will also be reflected in the particular code adopted. Thus the code contains a working model of the environment.

If the code stores sufficient information to form a model of the environment, its potential use in aiding survival is not confined to the provision of a more compact display of the sensary input. But to make full, predictive, use of these potentialities some additional facility for getting at this stored information seems to be needed. To return to the earlier example, what facility do we have for turning round the model engine in our brain so that we can look at the other aspect?

4. MODIFIED RE-CODING

So far the type of optimal coding envisaged has been that described by Shannon, Fano, and Huffman, in which the output is the smallest number of binary signals capable of carrying the information of the input. At first sight this seems to be what is needed in the nervous system, for nerve fibres transmit all or nothing impulses and thus seem to use a binary system. However, it has already been pointed out that the mean frequency of impulses is well below the optimal for information transmission even in peripheral nerve fibres, and there is some evidence which suggests that the

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mean frequency is even lower in the more central neurones (Galambos, 1954, *ref. 6*). Furthermore if the Shannon type of re-coding was occurring, one would expect to find the sensory pathways becoming more and more compact as the sensory information was coded on to fewer and fewer elements. This does occur in the retina, where some 10^8 sensory elements are connected to 10^6 nerve fibres, but as one follows the optic nerve into the brain there is no evidence of further compression on to a smaller number of nerves, but rather the reverse. The striate region of the cerebral cortex which is mainly, perhaps exclusively, concerned with vision, contains some 10^8 nerve cells; in other regions of the cortex there are about 6.5 x 10^9 cells (Sholl 1956, *ref. 20*) many of which must be partially concerned with visual information. Galambos (1954, *ref. 6*) gives striking figures showing how the number of nerve fibres available for auditory information increases as one follows the sensory pathway from ear to cortex.

These facts do not fit in with the idea that coding in the higher nervous system compresses information into a smaller number of nerve fibres, and suggest that, if optimal coding occurs, the output is not in the form of binary signals at the optimum frequency for information transmission.

For an engineer designing a communication link, the capacity of the channel is one of the factors under his control, and he can effect economies by coding his signals so that they require a smaller capacity. In the nervous system the number of nerve fibres available for a particular task must, to a large extent, be determined genetically. One may expect evolutionary adaptation to have performed part of the engineer's job in selecting suitable codes for the sensory signals, but such inherited codes obviously cannot be adapted to the redundancy of sensory input which is peculiar to each individual. Now although the number of nerve cells available is probably determined genetically, the number of impulses in the nerve cells is not, and some of the advantages of optimal coding would apply if the incoming information were coded - not onto the smallest possible number of nerve fibres each working at its optimal mean frequency - but into the smallest possible number of impulses in a relatively fixed number of nerves. This type of coding can be epitomised as *economy of impulses:* the nervous system will tend to code sensory messages so that they are represented, on the average, by the smallest number of impulses in the nerve cells available. There is an important difference between this type of re-coding and the Shannon - Fano - Huffman type; the latter does not distinguish between redundancy caused by non-optimal frequency of utilisation of the individual signs of the input message, and that which is caused by correlation between signs. If impulses rather than nerve fibres are economised, mean impulse frequencies of the output will be as low as the rate of inflow of information permits, and will thus possess maximum redundancy of the first type and minimum redundancy of the second type.

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A reversible coding device is described in the appendix which decreases the frequency of occurrence of a pair of binary output signs by getting rid of some of the redundancy caused by correlations between a pair of binary input signals.

5. EVIDENCE

So far some grounds for believing that the optimal coding of sensory information would be desirable have been given, arguing from the enormous quantity of information pouring in and from rather vague ideas about what the brain does with it. In this section some of the evidence in favour of the view that it does actually occur is sketched, but this is intended to show the kind of consequences of optimal coding which may be found experimentally, and is neither a claim that it has been proved to occur, nor a critical review of the evidence for and against it. The evidence comes from a number of sources.

(a) Introspection of sense impressions

This is a notoriously unreliable way of obtaining scientifically valid evidence, but it is immediately accessible to everyone, so it comes first. If the hypothesis is correct, the sensory messages reaching consciousness will have been partially re-coded, and will therefore have higher relative entropy and lower redundancy than the raw sensory messages. This seems to me likely to be true of the furniture of my own consciousness, and others may feel it is true also: if, however, somebody did not agree I don't think I could persuade him by verbal arguments. More objective evidence can be obtained by looking at some messages which do *not* reach consciousness but which are known to be impressed on the sense organs. Examples of this are the shadows of the blood vessels which run on the retina in front of the sensitive elements; the fact that if distorting or inverting spectacles are worn, after some days one ceases to be aware of the distortion or inversion; adaptation to the curious tone quality imposed on all sounds by the average domestic wireless set and so on. In all of these examples there are features of the sensory messages which are constantly repeated and are therefore redundant; a code which increased the relative entropy of the messages might be expected to reduce their prominence, and the fact that we cease to be conscious of them suggests that this re-coding does take place before sensory messages reach consciousness.

An experimental approach to this problem may be possible through the investigation of threshold sensations. These are perhaps the simplest elements of our consciousness, and according to the hypothesis they should tend to possess the highest possible relative entropy of a binary signal after the physical limitations of the stimulus and of the sense organs have been taken into account, and they should show a tendency to retain this property in a great diversity of stimulus conditions.

(b) From sensory neuro-physiology.

During the past thirty years various types of relation have been observed between an applied physical stimulus and the resulting pattern of nerve impulses. Physiologists have perhaps got used to these transformations and no longer think of them as something requiring further interpretation, but possibly they can be looked upon as examples of the principle of economy of impulses: the relation between the physical stimulus and the occurrence of impulses is such that the number of impulses used to convey information about the stimulus is lower than it would be with other, more straightforward, relations.

(i) Adaptation. When a sustained physical stimulus is applied to a sense organ the nerve fibre often responds with a brief burst of impulses which rapidly decreases in frequency and is not sustained for the duration of the physical stimulus. In the left half of *fig. 3* comparison of the trains of impulses shows the economy brought about by adaptation. But it can, of course, only be thought of as an economy when compared to a non-adapting ending, and even then only when the physical stimuli naturally applied to the sense organ are frequently of a long-sustained type. Nevertheless, where it occurs, adaptation would lead to economy of impulses and Adrian (1928, *ref. 1*), suggested that its function might be to prevent an excessive number of impulses reaching the nervous system.

(ii) Inversion. It can be seen from the right half of *fig. 3* that an adapting nerve fibre fails to signal the end of a sustained stimulus. This defect could be remedied by having one which discharged as shown in the bottom line, and such nerve fibres are found. In the eye of the scallop (Pecten) Hartline (1938, *ref. 9*) showed that one group of fibres discharged when a light was switched on and another group of fibres discharged at 'off'. A similar, but rather more complex, situation is found in the vertebrate eye (Hartline 1938, *ref. 8*; Granit, 1947, *ref. 7*). This arrangement might be thought of as making good some of the loss of information caused by adaptation.

(iii) Lateral inhibition. Adaptation increases the relative entropy of the nerve message by preventing many impulses being used to signal a physical stimulus which is constant in time. It is clear that physical stimuli will often be applied to many neighbouring receptors simultaneously, so there is a place for a spatial analogue of adaptation. The best worked out example of this occurs in the lateral eye of Limulus, where the arrangement shown in *fig. 4* has been deduced by Hartline and his co-workers *(ref. 10)*.

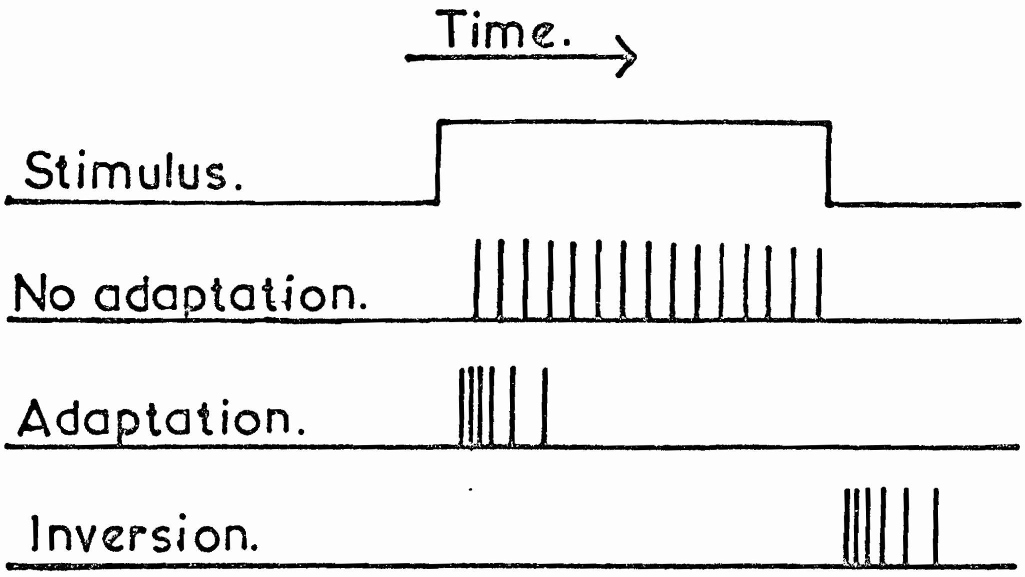

Fig. 3. Diagram showing that adaptation leads to economy of impulses when a physical stimulus is of long duration, and that inversion replaces information lost by adaptation.

Apparently each receptor in the array exerts an influence, graded according to the number of impulses it is itself producing, which reduces the number of impulses given by neighbouring receptor units. It will be seen that the effect is to decrease the number of impulses coming from a uniformly illuminated area, while the number coming from the borders of the area are relatively unaffected. A similar situation exists in the frog (Barlow 1953, *ref. 2*) and cat retina (Kuffler, 1953, *ref. 15*) and it has also been described in the auditory (Galambos 1944, *ref. 5*) and tactile (Mountcastle, 1957 *ref. 17*; Amassian, 1958, *ref. 21*) pathways.

One feature of lateral inhibition in the mammalian retina is of special interest: it is found when the retina is adapted to a uniform background light, but is absent after complete dark adaptation (Barlow, FitzHugh, and Kuffler, 1957, *ref. 3*). Now it is only when the uniform background is present that the correlated discharge of neighbouring receptors will tend to occur, so it looks as though lateral inhibition is not an invariant feature of the retinal organisation, but develops in the conditions where it can increase the relative entropy of the optic nerve signals. Perhaps

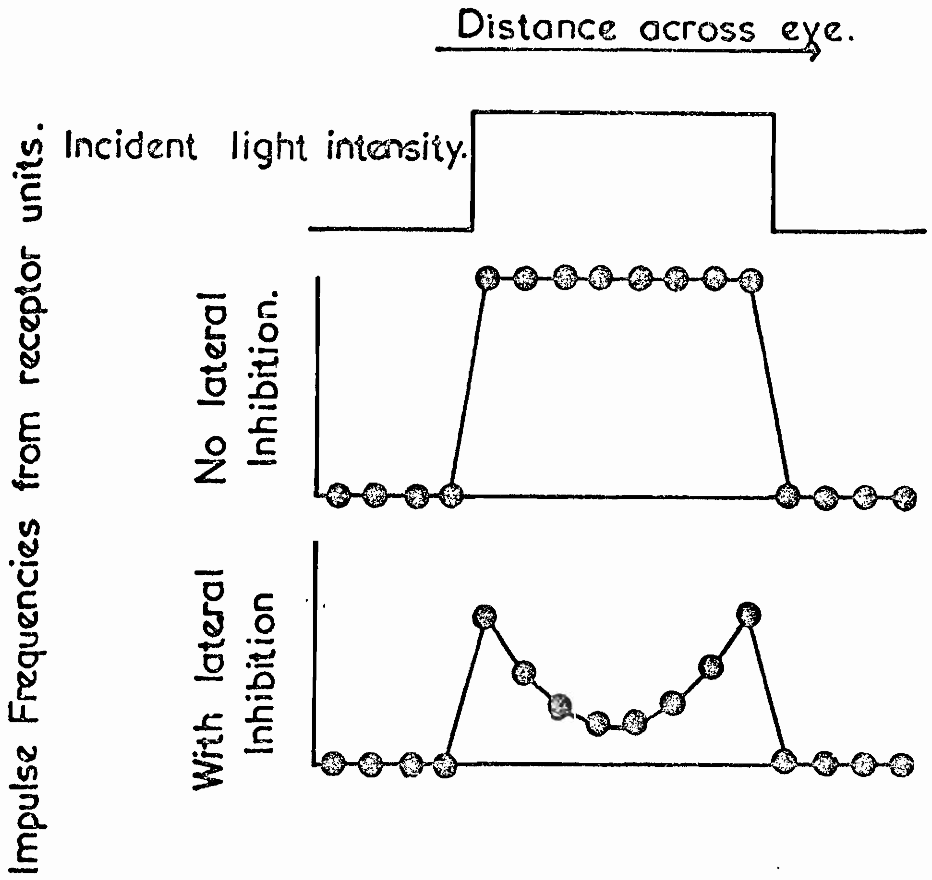

Fig.4. Diagram showing that lateral inhibition leads to economy of impulses in a uniformly illuminated area.

it is a simple example of "learnt" re-coding adapted to the redundancy which is present.

Adaptation, inversion and lateral inhibition may thus be devices used in the peripheral parts of sensory pathways to obtain signals of higher relative entropy. It is now possible to record the activity of more centrally placed neurones, but the nervous system has outwitted the physiologist who has so far been unable to determine the function of the cells whose nervous responses he has recorded. The model described in the appendix does a simple re-coding operation on two binary inputs, but it would be a difficult task to relate the output to past and present inputs without some hint about the purpose of the device. The reason, then, for putting forward the

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optimal re-coding hypothesis is the hope that it may be better matched to the subtlety of the nervous system than the simpler hypotheses at present entertained in physiology.

6. INTELLIGENCE

This word was added to the title in an incautious moment, but there are reasons justifying its inclusion. If it is accepted that the large size of the sensory inflow precludes its direct utilisation in the control of learnt motor actions, then the mechanism which organises this information must play an important part in the production of intelligent behaviour. In addition, when one considers the two main operations required for optimal coding there is a striking parallel with the two types of reasoning which underlie intelligence.

The outputs of a code can be thought of as logical statements about the input, and, if the code is reversible, these logical statements, taken together, are sufficient to determine the exact input. Forming these statements and ensuring that they fulfil this condition are straightforward problems of deductive logic. If the code is optimal, the output statements must be chosen so that they fulfil the additional condition that, on the average, they are the smallest possible number which suffices to determine the input (for the type of modified optimal code suggested in Section 4, the additional condition is that a fixed number of possible statements are chosen for the output in such a way that the smallest number, on the average, are asserted as true). The fulfilling of these additional conditions is not exactly inductive reasoning, but it is closely related to it, for both depend on counting frequencies of occurrence of events. Having been presented with 1000 white swans and no black ones, the relevant parts of a code would say "henceforth regard all swans as white unless told otherwise". Inductively one would say "all swans are white". The tools of logical reasoning appear to be the same as those needed for optimal coding, so perhaps they can be regarded as the verbal expression of rules for handling facts which our nervous system uses constantly and automatically to reduce the barrage of sensory impulses to useable proportions.

Finally it should be made clear that the transformations of sensory messages taking place in the nervous system must, in fact, fall a long way short of true optimal coding: information must be lost, and the final "display" must still contain redundancy. However, the fact that the image cast on the retina is not always sharp does not mean that the focussing of light by the eye is unimportant, and the suggestion is that optimal coding

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plays a part in the organisation of sensory information comparable with image formation in the working of the eye. However, even if this conjecture is correct, the means by which it is achieved, and such matters as the classes of redundancy which are easily and naturally utilised, and the classes which are not, remain largely undetermined.

APPENDIX

(In collaboration with P. E. K. Donaldson)

Object of device. To code reversibly and without delay a pair of binary inputs (A and B) onto a pair of binary outputs (X and Y) so that the redundancy of the output due to correlations is less than the same type of redundancy in the input.

Principle used. The information carried by the inputs will, in general, be less than the capacity of the input channels *first* because of redundancy due to correlations between them ($P(AB) \neq P(A).P(B)$): *second* because the frequency of signals in the individual channels is not optimum ($P(A) \neq \frac{1}{2}$ and $P(B) \neq \frac{1}{2}$). The principle used is to increase the redundancy of the second type, and so decrease that of the first type. A pair of outputs are sought which are reversibly related to the inputs, and one of which occurs with probability further from the optimum ($\frac{1}{2}$) than one, or both, of the inputs. The outputs carry the same information as the inputs, so that if such a pair can be found, the redundancy due to correlation between them must be less than is present in the inputs.

Possible Codes. There are four possible input states ($AB, A\bar{B}, \bar{A}B$, and $\overline{AB}$), and four possible output states ($XY, X\bar{Y}, \bar{X}Y$, and $\overline{XY}$). If the code is reversible these must be related to each other in a one-to-one manner, which can be done in 24 ways. Now since X corresponds to a pair of output states ($XY + X\bar{Y}$), the condition for activity in X must be the occurrence of either of a pair of the possible input states, and likewise for Y. There are six such pairs:- $AB + A\bar{B} = A$, $\bar{A}B + \overline{AB} = \bar{A}$, $AB + \bar{A}B = B$, $A\bar{B} + \overline{AB} = \bar{B}$, $AB + \overline{AB} =$ (A and B the same), and $A\bar{B} + \bar{A}B =$ (A and B different). In addition, for reversibility, the two pairs chosen must have a common member, for if this was not so X would always be active when Y was not active, and vice versa.

After a little cogitation it will be found that there are 24 possible codes, which fall into 3 groups each containing 8 codes, the groups differing from each other in the respect which interests us, namely the division of redundancy between correlation-type and non-optimal-frequency-type. One group does not differ from the input in this respect. The other two groups do differ, and they are made up of those 16 codes for which one or other of the outputs corresponds to either $AB + \bar{A}\bar{B}$ (A and B alike) or $A\bar{B} + \bar{A}B$ (A and B different).

Condition for success, then, is that either $P(AB + \bar{A}\bar{B})$, or $P(A\bar{B} + \bar{A}B)$, should differ from ½ by more than one or other or both of $P(A)$ and $P(B)$. This is not, of course, the same as the condition that A and B are correlated, so the recoding does not always reduce correlation redundancy when this is present. Successful recoding occurs for the smallest departures from zero correlation when either $P(A)$ or $P(B)$ is close to ½.

Method. The device is made up of 6 similar units each of which compares two probabilities and operates a relay according to which is greater (see circuit diagram, *fig*. 5).

(a) Probabilities are measured by charging a leaky condenser when A (or B etc.) = 1; hence they are weighted for recent events, the weights decreasing exponentially with lapse of time. These time weighted probabilities are called $P'(A)$, $P'(AB + \bar{A}\bar{B})$, etc.

(b) $P'(A)$ is compared with $P'(\bar{A})$, $P'(B)$ with $P'(\bar{B})$, and $P'(AB + \bar{A}\bar{B})$ with $P'(A\bar{B} + \bar{A}B)$. In each case a signal corresponding to the smaller of the pair is selected. Call these signals K, L, M.

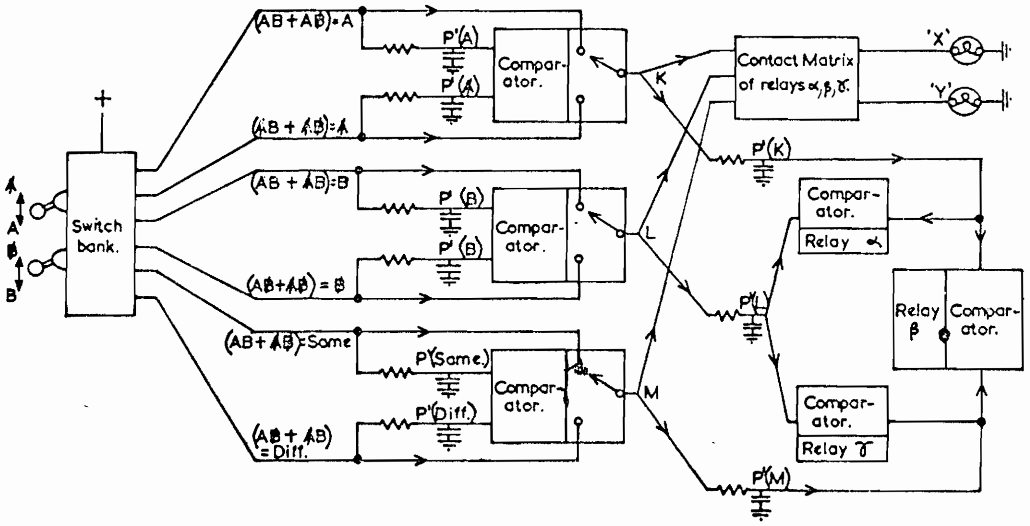

Fig. 5. Circuit diagram of recoding device.

(c) $P'(K)$ is compared with $P'(L)$, $P'(L)$ with $P'(M)$, and $P'(M)$ with $P'(K)$. Switching is performed according to the result of these comparisons so that

$$X \equiv \text{smallest of } K,\ L,\ M.$$

$$Y \equiv \text{next smallest of } K,\ L,\ M.$$

Result. The result of these operations is more specific than the original objective in that one particular code is chosen from a group of 8, any one of which would have met the requirements. The added specificity results from the fact that we have chosen outputs which occur *least* frequently, not *most* frequently, and have arranged that $P(X)$ shall be less than $P(Y)$.

Note that if there is any logical relation in the inputs (e.g. $\bar{A}B = 0$), then the outputs become mutually exclusive ($P(XY) \doteq 0$). If there is a double relation (e.g. $A\bar{B} = 0$ and $\bar{A}B \equiv 0$), then only one output channel operates ($P(X) = 0$). The device might be roughly described as one which determines inductively what logical relations, if any, are obeyed by its input. If two such relations are found, one output channel is not used; if one is found, the two outputs become mutually exclusive; if none is found, but there is statistical correlation between the inputs, it will sometimes find outputs which are less correlated.

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