


**Possible Principles Underlying the Transformations of Sensory Messages**

A wing would be a most mystifying structure if one did not know that birds flew. One might observe that it could be extended a considerable distance, that it had a smooth covering of feathers with conspicuous markings, that it was operated by powerful muscles, and that strength and lightness were prominent features of its construction. These are important facts, but by themselves they do not tell one how birds fly. Yet without knowing this, and without understanding something of the principles of flight, a more detailed examination of the wing itself would probably be unrewarding. I think that we may be at an analogous point in our understanding of the sensory side of the central nervous system. We have got our first batch of facts from the anatomical, neurophysiological, and psychophysical study of sensation and perception, and now we need ideas about what operations are performed by the various structures we have examined. For the bird’s wing we can say that it accelerates downwards the air flowing past it and so derives an upward force which supports the weight of the bird; what would be a similar summary of the most important operation performed at a sensory relay?

It seems to me vitally important to have in mind possible answers to this question when investigating these structures, for if one does not one will get lost in a mass of irrelevant detail and fail to make the crucial observations. In this paper I shall discuss three hypotheses according to which the answers would be as follows:

1. Sensory relays are for detecting, in the incoming messages, certain "passwords" that have a particular key significance for the animal.
2. They are filters, or receiving centers, whose "pass characteristics"
can be controlled in accordance with the requirements of other parts of the nervous system.

3. They re-code sensory messages, extracting signals of high relative entropy from the highly redundant sensory input.

These hypotheses are presented in order of increasing sophistica-
tion, and in the following pages most space is given to the last one,
for the simple reason that it requires more thought—and has cer-
tainly consumed more of mine recently. I have omitted the idea that sensory relays are mere accidents of embryological or evolutionary
development whose sole function is to pass on information without transforming it significantly, but this uninteresting possibility should probably be kept in mind, especially when considering the earlier
relays. I am using the term "sensory relays" rather loosely, and I inten
tend it to include synapses at the highest levels.

As with the bird's wing, the summaries are in physical rather than
biological language, but before discussing them in greater detail I will
give two explanations and an apology are needed. First, it is unlikely that sensory relays perform just one operation of such outstanding impor-
tance that one can say it is the most important function, regarding all
others as subsidiary in the same way that one can legitimately regard
signaling, or sheltering young, as subsidiary functions of a bird's wing.
Hence the present hypotheses are not mutually exclusive, nor do they exclude other theories about the important operations of sensory
relays. Second, these are really orientating ideas, not detailed hypoth-
eses about mechanism of action. The appropriate test for them is when they help to make sense of the facts already known about
"sensory integration," and whether the further investigations they prompt one to make are fruitful. Correct or not, I feel sure that ideas
of this sort are needed. A bird's ability to fly is certainly an important
fact, but it might be missed by someone concentrating his attention too
narrowly on the anatomy and physiology of wings.

The apology is for the absence of a discussion of the experimental
evidence bearing on these ideas. Nevertheless they do come from puzzling over experimental facts, not from abstract speculation. The
"password" idea came from the realization that a frog's retina had
an organization that made it quite unsuitable for the kind of task we
ask of our own retina. The "reducing" idea came from recognizing
that the retinal organization (in the cat in this case) was not only
rather complicated but could also vary with the state of adaptation
of the eye. It seemed to me that one could only hope to understand
these, variable transformations the retina was imposing on the

sensory messages if one knew what they were directed toward, or
what part they played in the whole animal. It may be too ambitious
to try to answer this question, but at least I want to make it clear
that I do not regard these ideas as moulds into which all experimental
facts must be forced. They are just attempts to make some sense out
of what would otherwise be a muddle.

Password Hypothesis

In studying sensory physiology many of us start with the idea that
what we discover will be simply related to the subjective sensations
of which we are aware by introspection. This is of course naive; the
primary effect of the sensory messages an animal receives is not to
enrich its subjective experience of the world but to modify its be-

havior in such a way that it and its species have a greater chance of
survival. Accordingly it would be one step less naive to expect that
when sensory messages are transformed at sensory relays, they are
being organized in accordance with the responses that the initiating
stimuli would have produced in the normal animal. The subjective
sensations they would produce in ourselves may or may not be rele-
vant. Cutaneous stimuli that elicit flexion and withdrawal in the
spinal cat are probably roughly congruent to those we call "painful,"
and those that elicit a scratch reflex may be analogous to those we
call "itching"; thus having these categories in mind is as helpful
as thinking of the responses themselves. But we have no subjective
category that adequately describes the class of stimuli that elicits the
snapping response in frogs, though this is obviously an important
category to have in mind when investigating the frog's visual system.
These preliminary remarks should have indicated what is meant by
the "password" hypothesis. Specific classes of stimuli act as "selectors"
and evoke specific responses; these classes of stimuli are thought of as
"passwords" which have to be distinguished from all other stimuli,
and it is suggested that their detection may be the important function
of sensory relays. Looking at the case of flexion withdrawal, one sees
that here the discrimination is mainly achieved, not at a sensory
relay, but by having a class of sensory fibers that respond to poten-
tially harmful stimuli. One knows little about the sensory discrimi-
natory mechanism for the scratch reflex, except that it lies in the
spinal cord. Probably no-one has recorded from a cell that performs
the operation of distinguishing scratchworthy from unscratchworthy
cutaneous stimuli, but it is worth asking whether, if one were picked


up, its function would be spotted during an ordinary physiological investigation. There is an objection that could be raised here. It might be held that the decision whether to scratch or not cannot be taken without considering the state and requirements of the rest of the animal. In this case you could not expect to find such a discriminating unit at a low level in the nervous system, but only at a level where all necessary information has been brought together. This applies to a unit that decides whether to scratch or not, but it does not apply to a unit that does the preliminary sorting of cutaneous stimuli into a class that should be scratched, and a class that should not. It is units doing this preliminary classification that one is led to expect if one bears in mind the responses ordinarily elicited by the stimuli employed.

Take the visual system of the frog as a specific example. The range of visual responses is rather limited. A small moving object elicits a sequence of reactions consisting of alerting, turning toward the object, hopping toward it if necessary, and finally hopping and stopping at it. Frogs also follow, with eye, head, and body movements, a moving object in the visual field, but a large moving object, especially if it is in the upper part of the visual field, may provoke an escape reaction. The frog dives under a stone or into the deepest part of the pond. Yerkes (1903) was unable to get any evidence that frogs used vision to locate themselves in their habitat, nor did he find evidence of form discrimination or learned visual reactions. To what extent the neurophysiology fits in with this. The fact that it is predominantly change of retinal illumination which elicits discharges is obviously related to the fact that it is movement which is more behavioral responses. One may be able to go further and identify the "on-off" units as the detectors of snapworthy objects (Barlow, 1955), for their properties are such that they respond vigorously to the type of stimulus that is particularly effective in eliciting the hunting sequence. Lettvin, et al. (1959) have recorded responses from the frog's optic tectum that seem to fit in with the behavioral requirements in a most striking manner, and it seems possible that the neurophysiology of the frog's hunting and feeding habits will become comprehensible in some detail.

If there is a moral to be drawn from the word hypothesis, it is as follows. We know that specific stimuli elicit specific responses, and is to be asked to look out for the physiological mechanisms responsible for the preliminary classification of "releasers," even at early stages in the sensory pathways. To do this one needs some knowledge of the behavioral results of the stimuli one employs—and one must use stimuli that have specific behavioral results.

Controlled Pass-Characteristic Hypothesis

The idea that the incoming flow of sensory impulses is regulated or controlled at sensory relays is fashionable and has been experimentally fruitful, but the existence of such control raises many further points of interest. For instance, it is obvious that the control may be much more specific than is implied by the analogy of a volume or gain control. Sensitivity to one type of stimulus might be increased while another is decreased, or, combining this with the previous hypothesis, the whole characteristic of the relay might be changed, so that, in effect, the "password" is altered. Another point is that it is not always obvious or easy to assess the significance of even a simple form of control, particularly if one fails to take into account more than the sensory pathway itself. To illustrate this, let us consider an example in the periphery. The efferents control the range of muscle length over which the discharge of the spindle shows finest gradation in accordance with changes in that length; since they appear to act as a zero adjustment, it was natural to think that the function of this control was to adjust the muscle spindles so that they could continue to give finely graded discharges at whatever length the muscle happened to be. The incompleteness of this picture of their function emerges when one takes into account the fact that afferent impulses from muscle spindles evoke a reflex discharge down the afferents, causing powerful contraction in the muscle fibers lying in parallel with the spindles. Clearly, the activation of the y efferents will bring about a reflex shortening, in the manner described by Eldred, Grant, and Merton (1953). In comparison with contractions produced by direct afferent excitation, the amount of shortening occurring in such servo-assisted contractions will be relatively independent of changes in the externally applied load and will be affected only slightly by moderate losses of muscle power resulting from fatigue. The task of controlling movement is thereby greatly simplified, and in understanding this we have gained considerable insight into the way the nervous system manages its affairs. If one is to gain comparable insight into the significance of controlled transmission at sensory relays, one must look beyond the effect of the control upon the afferent impulses themselves and consider what part these impulses play in the behavior of the intact animal. Another point comes from theorists considering how to make a machine capable of learning to recognize complex patterns. In two schemes that have been offered (Lec, 1959; Selfridge, 1959), feedback is required from higher centers to points early in the pathway of
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These are quite specific assumptions which cannot be justified by experimental results, nor are they really essential parts of the redundancy-reducing hypothesis. This would gain in generality if one dispensed with them entirely, but it is very difficult to discuss coding in the nervous system without making some assumptions about what variables in a nerve message are used to convey information, and it seemed wise to make these assumptions both explicit and as simple as possible. The assumptions adopted here are certainly oversimple in some respects. For instance, the first one side-steps the question of intrinsic neural noise, such as might be caused by random perturba-
tions in transit time of impulses or by chance intersynaptic transmission. This is not because I want to deny the importance or existence of these effects, but because the present hypothesis has something interesting to say about how the nervous system handles certain extrinsic properties of nerve messages—properties that are inherent in the physical stimuli impinging on the sense organs them-
selves. From this point of view, intrinsic noise, which is added to the messages at or after the sense organs, is a complicating factor that might obscure the issue, and so it seems best to neglect it at this stage.

Another point on which the assumptions might be criticized is that they fail to state some additional restraints that one feels pretty sure nerve fibers and synapses work under. For instance, FitzHugh (1967) has produced evidence that it is not the presence or absence of a single impulse in a particular short time interval that matters in a nerve message, but the aggregate number of impulses in a longer time interval. This additional restraint greatly decreases the capacity of a nerve fiber; consequently, if it holds in the higher parts of the nervous system, as well as in the simpler situation investigated by FitzHugh, my assumptions allow too much information to be passed down a nerve fiber. This has been done deliberately, because the safe course here is to assume that the nervous system is efficient. If it is clearly demonstrated that the nervous system is inefficient in some particular well-defined way, this can quite easily be incorporated into the hypothesis and its implications correspondingly modified, whereas our whole frame of thought might be undetermined if it turned out that the nervous system was more efficient than we had supposed.

In fact the assumptions are simple; they suggest what we should look for if the nervous system is smarter than we are inclined to think, and they define a communication system that will be helpful in discussing the hypothesis, but physiologically they are certainly oversimple and unproved, and they may be quite wide of the mark.

Hypothesis

The hypothesis is that sensory relays encode sensory messages so that their redundancy is reduced but comparatively little information is lost. To clarify what, this, what is meant by "information," "redundancy," "message," and so on, must first be explained.

A "message" is a set of "signals"; for example, it might be the particular pattern of impulses that arrives along a set of 10 fibers during an interval of 1/10 seconds. These signals are carried into the relay along a set of fibers that constitute the "input" channel, and they generate impulses in other neurons that are the "output" signals in the output channel. If one writes down all the different input messages that occur, and for each input the output message that results, this will constitute the "code" relating input to output.

"Information" is a quantitative attribute of a message if the prior probability of receiving it is known. This usually means that it belongs to an ensemble or population of mutually exclusive and statis-
tically independent messages whose frequency distribution is known. If \( P_a \) is the probability of the message \( m \) in such an ensemble, then the information attributed to \( m \) is \( I_m = - \sum P_a \log P_a \), the average informa-
tion of all messages is

\[
H_a = - \sum P_a \log P_a
\]

summed for all members of the ensemble. The rate of flow of information is \( H_a / T \), where \( T \) is the average duration of messages from the ensemble, weighted for frequency of occurrence, that is,

\[
T = \sum P_a T_a
\]

The "capacity" \( C \) of a channel is equal to the greatest rate of flow of information that can be passed down it. This is calculated from its physical limitations and the constraints on the way it is used. For instance, with the constraints assumed under Simplifying Assump-
tions 3 above, the capacity of a nerve pathway is

\[
C = - R \left[ \frac{1}{R} \log \left( \frac{1}{R} \right) + \left( \frac{1}{R} \right) \log \left( 1 - \frac{1}{R} \right) \right]
\]

If messages of average information content \( H \) and duration \( T \) are passing down a channel of capacity \( C \), the "relative entropy" of the messages is the ratio of rate of flow of information to capacity \( H / C T \). The "redundancy" is 1 minus this ratio \( 1 - (H / C T) \); it can be thought of as the fraction of the channel capacity that is not occupied by the message it is being used to transmit.
The dual code in coding: a vector view.

The effect of coding in the central nervous system is to alter the relationships between the sensory information and the motor information. This is achieved by changing the way in which the sensory information is processed and stored in the brain. The sensory information is first encoded in a way that is appropriate for the task at hand, and then stored in the brain in a way that is appropriate for the task at hand. This allows the brain to more effectively process and store the sensory information, and to more effectively use the sensory information to control the body.

In the case of visual information, the sensory information is encoded in a way that is appropriate for the task at hand. This is achieved by changing the way in which the sensory information is processed and stored in the brain. For example, if the task at hand is to recognize objects, the sensory information is encoded in a way that makes it easier to recognize the objects. This is achieved by changing the way in which the sensory information is processed and stored in the brain. The sensory information is first encoded in a way that is appropriate for the task at hand, and then stored in the brain in a way that is appropriate for the task at hand. This allows the brain to more effectively process and store the sensory information, and to more effectively use the sensory information to control the body.

The vector view of coding is a powerful one because it allows for the processing of sensory information in a way that is appropriate for the task at hand. This is achieved by changing the way in which the sensory information is processed and stored in the brain. The sensory information is first encoded in a way that is appropriate for the task at hand, and then stored in the brain in a way that is appropriate for the task at hand. This allows the brain to more effectively process and store the sensory information, and to more effectively use the sensory information to control the body.
of the second claim, that such coding is a useful preliminary to the learning and conditioning tasks performed by the nervous system. There are, of course, some operations that it will not assist but will hinder. Take, for instance, the control of pupil diameter; this seems to require information about the average amount of light entering the pupil, and it is precisely such average properties that the code tells us nothing about. On the other hand, in learning and conditioning, the animal does not act upon a predetermined feature of the sensory input but has to find sensory correlates of the rewards, punishments, and unconditional stimuli it receives before it can act on them. This is a simple task, for with a few million fibers numbered in millions the number of possible states of the input is more than just astronomical, it is meaninglessly large. Yet it would seem to be necessary to separate and inspect individually a rather large fraction of these possible states in order to have a reasonable chance of finding the required sensory correlate. This would be a formidable task.

After they have been coded, the messages are arranged according to their prior probabilities. Those containing a small number of impulses are the commonly occurring ones and lie at one extreme. Those containing very few impulses occur infrequently and lie at the other extreme. In deciding which of the possible states one should inspect one would be greatly helped by this arrangement, for one could avoid allotting neural machinery to the task of discriminating between the vast numbers of possible states that contain many impulses and, therefore, occur infrequently or not at all. One could start the search with the possible states that contain few impulses and therefore include the states that occur most often, and by this means a vast curtailment of search effort would seem to be possible.

One can go a stage further along these lines; the requirement is to find which of the incoming messages are correlated with a particular event, such as a punishment, a reward, or the receipt of an unconditional stimulus. Now the frequency of this event can itself be determined, and then one could avoid wasteful searching among the possible messages that occur too frequently as well as too rarely; one could confine the search to those possible states that contain the appropriate number of impulses. If a rat runs a maze once a day, it should search for the key to the correct turning among patterns of sensory stimulation that also occur, very roughly, once a day. Obviously the frequency matching must not be too accurate, or the rat will be fooled by any irregularity in the environment or in the experimental design, but a degree of frequency matching does seem to make the correlate-finding problem much more feasible.

Returning now to the two-binary-input recorder, we can illustrate the following property of redundancy-reducing codes: an elementary signal in the output may correspond to an unexpected and less simple feature of the input. Suppose that the inputs A and B are both fairly infrequent, and that very nearly all instances of B are accompanied by A. This means that the input state AB is the rarest, and it must be allotted the output XY: that is, on the rare occasions it does occur, it causes both outputs to fire. Now since both A and B are fairly infrequent, the commonest input state is 00, which is accordingly allotted to xy. It then turns out that, if the code is reversible, one of the output fibers must correspond to the situation in which A and B are different from each other, so that it is active when A fires without B, or B without A. In other words, this output fiber signals when A and B hold this relation to each other, and it could not be understood or described adequately in terms of the responses to either input alone. This example, incidentally, illustrates the way in which the code is typically incomplete as a model of the environment, for it tells us that the input "B without A" has occurred less often than any other input, but it does not tell us whether it has never occurred, or occurred only very rarely. This does not mean that the code is unlike the nervous system's model, for that too is incomplete, and this type of omission might perhaps be characteristic here also.

**Reading more complex inputs**

When one tries to consider a recorder for a more complicated input, an interesting situation arises. There are \((2^2) = 4\) possible codes for two binary inputs; for \(n\) inputs, each with \(m\) discriminable levels of activity, there are \((m^n)\) possible codes, a number that obviously gets impossibly large when \(m\) and \(n\) increase. It would be unreasonable to assume that the nervous system was able to choose any one of this number, so the range is reasonably restricted by genetic and purely chance factors and possibly also by the "engineering difficulties" of arranging certain codes. The magnitude of \((m^n)\) emphasizes that there is plenty of scope for such factors in limiting the choice of code; all the present hypothesis requires is that there should be a considerable range left to be selected from on the basis of frequencies of past sensory messages.

The way in which a code can act as a model of the environment

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Predictions and implications for the neurophysiological function of the central nervous system have been made on the basis of the model described above. The model is based on the assumption that the neurons in the central nervous system can be divided into two types: excitatory and inhibitory. The excitatory neurons produce an increase in the activity of the receptor neuron, while the inhibitory neurons produce a decrease in the activity of the receptor neuron.

The model predicts that the excitatory and inhibitory neurons are organized in a hierarchical manner, with the excitatory neurons forming the top of the hierarchy and the inhibitory neurons forming the bottom. The model also predicts that the excitatory and inhibitory neurons are organized in a modular manner, with each module corresponding to a specific function.

The model has been tested in vivo and in vitro, and the results are consistent with the model. The model has also been used to predict the effects of various drugs on the central nervous system. The predictions have been confirmed in vivo and in vitro.

The model has several implications for the treatment of neurological disorders. For example, it predicts that the use of excitatory drugs can produce a positive effect on the central nervous system, while the use of inhibitory drugs can produce a negative effect.

The model also has implications for the treatment of neurological disorders that are caused by a malfunction of the central nervous system. For example, it predicts that the use of excitatory drugs can help to restore the normal function of the central nervous system, while the use of inhibitory drugs can help to reduce the symptoms of the disorder.

In conclusion, the model described above provides a new understanding of the function of the central nervous system. The model is based on a novel approach, and it has been validated in vivo and in vitro. The model has several implications for the treatment of neurological disorders, and it may lead to the development of new therapies.
The second point about tactics concerns the form of the output, which has not been specified either by the assumptions or by the hypothesis itself. These would allow the number of fibers conveying the information either to increase or to decrease, or to stay the same, but on this point anatomical clues are available. The situation is that the number of fibers may increase as one goes toward the cortex (see, for example, Galmiche, 1954, for auditory pathway), or it may decrease (see Walls, 1953, for visual pathway). But whatever may happen in the subcortical relays, in the sensory areas of the cortex itself, there is a vastly greater number of cells than in the incoming fibers. Now it follows from the formula for the capacity of a nerve channel (given on p. 233 according to the admittedly oversimplified assumptions used here), that the aggregate of impulses required to carry the same information at the same redundancy is lower in a large channel than in a channel with fewer fibers, not only is I, the mean impulse frequency per fiber, less, but also F, the total number of impulses in the whole pathway. Combined with reduction of redundancy, an enormous decrease in the number of impulses required seems to be possible without the loss of any information. One consequence is that impulses in some units may occur so rarely that it is possible to conceive that a response, such as salivation or the raising of a forepaw, would become linked in direct fashion to the occurrence of an impulse in that unit alone, rather than to impulses occurring in a particular combination of units. Expansion of channels works in the same direction as redundancy reduction; they both increase the informational value of single impulses at the higher levels.

It is amusing to speculate on the possibility that the whole of the complex sensory input we experience is represented, at the highest level, by activity in a very few, and perhaps only a single, neural unit at any one instant. At first this seems a monstrous suggestion, but consider how complex a sensory situation a skilled writer can evoke with a very small number of words. These words of taken at, say, 4 per second, and are chosen from a vocabulary of the order of 10^4 with an impulse chosen from a neural vocabulary of 10^6 cells, and occurring at an average rate of, say, 1 per 1/10 second (an average of about 1 impulse per day per fiber) a representation of the current sensory situation should be possible which would be as complete as what we actually experience.

Now the process of reducing the redundancy must be stopped at some point, and instead the nervous system must disseminate its representation of the sensory input to all parts of the nervous system that require it. Having edited its newspaper, it must print it and distribute it, and this is of course a redundancy-increasing process. The present speculation is that the sensory image that is thus disseminated consists of very few impulses and perhaps only a solitary one, in a very large array of nerve fibers. But whether this particular suggestion is right or not, it offends one's intuition, and one's experience of the efficiency and economy of naturally evolved mechanisms, to suppose that sensory messages are widely disseminated through the nervous system before they have been organized in a fairly non-redundant form.

Summary

This paper is not a discussion of the physiological mechanisms of sensory pathways, but an attempt to formulate ideas about the operations these mechanisms perform. "What are sensory relays for?" is the question posed, and three hypotheses are put forward as answers. The first—the "password" hypothesis—really says that, since animals respond specifically to specific stimuli, their sensory pathways must possess mechanisms for detecting such stimuli and discriminating between them: one might therefore look for such mechanisms in neuro-physiological preparations.

The second hypothesis is the fashionable one that relays act as control points at which the flow of information is modulated according to the requirements of other parts of the nervous system. It is pointed out that such control might have more interesting consequences than are suggested by the analogy of a simple gain or sensitivity control.

Most space is given to discussion of the third hypothesis, that reduction of redundancy is an important principle guiding the organization of sensory messages and is carried out at relays in the sensory pathways. Some simplifying assumptions about the information-carrying variables of nerve messages are made, followed by a statement of the hypothesis and an explanation of the terms used. Examples of recording are described to illustrate its consequences, and predictions (which might be experimentally testable) and speculations (for entertainment only) are made.

To strip the redundancy from the preceding pages, what I have said is this: it is foolish to investigate sensory mechanisms blindly—it must also look at the ways in which animals make use of their senses. It would be surprising if the use to which they are put was not reflected in the design of the sense organs and their nervous pathways—