A Note on Temporal Coding as a Mechanism in Sensory Perception

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Neurone theory and the concept of the all-or-none nerve impulse are fundamental to modern neurophysiology; but the simplest ideas derived from these lead to the difficulty as to how complex sensory perception is possible through such limited structure. Recent studies suggest the possibility that in the visual system of man over-all temporal patterns of activity may be used for the transmission of certain sensory information. It is possible that this temporal coding may arise from the differing nerve impulse conduction velocities that exist in a nerve fiber bundle. Such a coding system may have a significant part to play in the general functioning of the nervous system.

Sensory perception in man is a complex set of processes. We gain this impression from our own subjective experience and from a study of the behavioral patterns that follow such perception. At the same time it is now accepted that the discrete nerve impulse is the basis of the coding system that transmits sensory messages from the receptor organs to the central nervous system.

If the simplest arrangement of this system is proposed—involving a code based on spatial and frequency distributions of the nerve impulses—it is difficult to correlate the complexity of sensory perception with known nerve structure. What makes this especially true is the limited number of nerve fibers in a given sensory channel; the all-or-none basis of the impulse itself; and the limited frequency, rarely more than 300/sec and usually less, at which impulses can be carried in a single nerve fiber.

In practice this lack of correlation between sensory perception and nerve structure is seen most clearly in the relation of man to a technical environment. In such environments human control is often dependent on complex perceptual patterns changing rapidly with time. A typical example would be a crew flying an airplane at several times the speed of
sound, a task which men are quite capable of performing successfully with a minimum of automatic aid.

This problem of linking a complex environment with a perceptual pattern can be partially resolved by assuming that in the nervous system other codes are used besides the usual spatial and frequency patterns of nerve impulses. Recent experiments in this laboratory seem to give further evidence that there are mechanisms within the nervous system capable of producing alternative codes. In the following paragraphs the significance of these results and their relation with previous knowledge are discussed.

Some of these experiments were concerned with vision, the sense which in many situations is the dominant one and which produces perceptual patterns with many properties—brightness, form, depth, movement and color among them. All these perceptual properties follow from light stimulating the sensory cells in the retina of the eye. There is considerable evidence that the brightness of the stimulus is transmitted in terms of nerve impulse frequency in the fibers of the optic nerve (Hartline and Graham, 1932) and that its geometrical form results from the spatial relationship of the stimulated retinal cells and their associated fibers.

Perception of stimulus hue presents a more difficult problem. The most straightforward proposal is that there exists an analytical system in the nervous layers of the retina to break down the spectral characteristics of the stimulus into separate groups—three in the tristimulus theories—and it is then often assumed that these characteristics are transmitted along independent sets of nerve fibers of the optic pathway to make contact with separate structures within the brain. Such a proposal makes a great demand on the capacity of the sensory system, which already appears limited in relation to the messages it carries.

In these experiments on visual perception we have shown that in man there is a time interval between stimulus presentation and stimulus perception that appears to depend on stimulus wavelength. The visual stimuli used were flashes of light produced by electronic flash tubes. They lasted only a few microseconds and their spectral characteristics were controlled by narrow band filters. The stimuli were presented to subjects with normal or defective color vision in an experimental procedure that was briefly as follows: blue, green, and red light flashes were shown in pairs; the flashes in each pair could be presented simultaneously or with a time interval between them. Under controlled experimental conditions which included making the complete stimulus fall on a rod-free area of
the retina the subjects were asked to report the apparent order of the
two flashes. Subjects were able to perform this task and give results that
were repeatable within a few milliseconds.

In almost all cases, to obtain a report that both flashes of light were
perceived together, there had to be a time interval between the two parts
of the stimulus. This interval was a measure of the differential latency
between those two colors. The colored flashes that were used could be
regarded, by virtue of their short duration of a few microseconds, as im-
pulsive stimuli; they evoked a perceptual image that was spread over a
considerable period of time, of the order of 50–100 msec. Of particular
importance in this present context, it seemed possible that there were
peaks within this response which could have given rise to an impression
of color order when stimuli with different wavelength characteristics
were displayed at the same instant in physical time; for example to sub-
jects with normal color vision the apparent order of simultaneous red
and blue flashes was red followed by blue, and the latency differential
was of the order of 10–15 msec.

A possible contributing factor producing this perceptual behavior is
that the rate at which the sensory message is transmitted from the eye
to the brain is dependent on the wavelength of the stimulus. This is in
accord with the results of electrophysiological studies of the visual path-
way in anesthetised cat (Lennox and Madsen, 1955).

The conduction velocity of a nerve impulse is associated with the nerve
fiber diameter (Erlanger and Gasser, 1937), internodal length in medul-
lated fibers, and other factors whose contribution is not precisely known.
Since any nerve or fiber tract is normally built up of fibers of differing
structural configuration, the time sequence of events at the receiving
end will differ from that at the transmitting end. Thus in addition to the
over-all time of transmission along the length of the nerve-fiber tract,
there will be individual differences depending on the fiber structure so
that a single event at one end will give rise to a temporal pattern at the
other. The shape of this pattern will depend on the degree of activity in
the individual fiber groups. By this mechanism we can have, quite apart
from a simple frequency code along individual fibers, an additional, over-
laid code based on temporal factors (Fig. 1).

If it is admitted that there exists within the nervous layers of the retina
a mechanism for spectral analysis, then a possible mechanism for the
transmission of hue can be envisaged: the fibers of the optic nerve might
be in contact with the retinal layers in such a way that a given spectral
Fig. 1. Due to the different rates of conduction along the nerve fibers of the fiber bundle a single stimulus at one end will generate a temporal pattern at the other end; the shape of this pattern will depend on the degree of activity in the individual fiber groups.

distribution of input gives rise to nerve impulse transmission predominantly along nerve fibers that can be related to the input spectrum, the degree of activity of a fiber being functionally dependent on its associated conduction velocity compared with the stimulus wavelength. At the brain, the over-all effect of impulsive stimulation would be a temporal pattern with an outline that could be related to the spectral characteristics of the visual stimulus.

If such a mechanism forms the basis of normal color perception further apparatus would be necessary to generate discrete stimulation of the retinal receptor cells, otherwise the temporal coding would be lost in continuous stimulation. It could be suggested that the continuous, involuntary tremor of the eyeball, which has been shown to be necessary for visual discrimination and color perception (Ditchburn, 1956), may transform continuous visual inputs into sets of discrete stimuli in the sweep from one receptor to the next.

Experiments in this laboratory have confirmed the presence of this eyeball tremor. In this case the electrical potentials associated with eyeball movement were recorded on a low-frequency magnetic tape system. Analysis of the records showed frequency components close to those of the alpha rhythm of the electroencephalogram but they were shown to be produced by actual movement of the eyeball. Nevertheless the similarity may be a pointer to the importance of temporal factors in perception.

The possibility that such a scheme plays a part in the perception of
stimulus hue raises several interesting points. First, it provides an extension to the triple-pathway theories of color vision, and in so doing helps to overcome the conflict between these theories and the information capacity of the associated multiple transmission pathways and the degree of structural multiplication that is needed in the brain. Second, it gives a further functional meaning to the differences in conduction velocity along nerve fibers. Third, it suggests a coding scheme that might be used in other parts of the nervous system; for example, is temporal coding used in the transmission of sensory information from the skin to the brain with the pattern of the response being related to the finer and yet unexplained details of cutaneous perception? Pain as a single sense behaves in this way to give rapid perception by way of an immediate pain followed by a duller delayed pain (Lewis and Pochin, 1937).

That a temporal pattern at the cortex arises from the skin receptors associated with the cutaneous sense may give practical significance to the involuntary tremor of the peripheral musculature—a tremor which in the fingers and other parts of the body we have confirmed to have a dominant frequency component of 10 cps.

It must be admitted that some of the above is of a conjectural nature. But modern advances in technology make such speculation a practical necessity. The number of problems posed by human control in extreme conditions increases rapidly and some of these require practical solution urgently. Knowledge of nervous system mechanisms must be of considerable help in obtaining these solutions.

In such examples as man in control of a very high-speed machine or man working in a vibrating environment where perceptual disorder and subjective discomfort can occur, the relation of time in the external environment to temporal mechanisms within the central nervous system must play an important role. If in particular the transmission of sensory information incorporates a temporal mechanism, as is suggested above, failure of this mechanism may be a significant factor in the difficulties so often encountered in practical situations.

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References


