Acta Biol. Exper. (Warsaw), Vol. 27, No. 2 pp. 1967, 147—161, 1967

SOME NEW IDEAS CONCERNING THE PHYSIOLOGICAL MECHANISMS OF PERCEPTION*

J. KONORSKI

Department of Neurophysiology, the Nencki Institute of Experimental Biology Warsaw 22, Poland

(Received December 5, 1966)

I

If we make a general survey of the neurophysiological studies on the functioning of afferent systems we may see that they can be classified according to two principles of division.

First, they differ in respect to the indicators utilized in particular investigations. In some of these investigations the behavioral responses of the organism are used, included here are the verbal reports of the human subjects serving in the appropriate experiments, in other investigations evoked potentials of the afferent pathways and of the projective cortical areas are recorded. Of course, with the recent growth of electrophysiological methods, the latter methods of research take an upper hand and are gradually dislodging the former methods.

Secondly, the investigations of afferent systems differ in respect to the stimulated structures. Here we have either those studies in which receptors are stimulated by natural stimuli, or those in which particular nerve trunks or nerve fibers are stimulated by electric currents. Again we may observe that while in the earlier periods of neurophysiological research work, say in the time of Pflüger and Sherrington, the natural stimulation of receptors was dominant, in recent years most investigators

* According to the evening lecture delivered in National Institutes of Health on 25th May 1966. This lecture was based on material from a forthcoming book of the author "Integrative Activity of the Brain", to be published by the University of Chicago Press.

make use of electrical stimulation of afferent nerves. This latter way of experimentation was introduced because electric stimuli are certainly easier to manipulate and are considered more reliable in their exact reproduction than natural stimuli impinging upon receptors. One may ask, however, whether that which seems more elementary and reliable to the experimenter is also more elementary for the organism — whose evolution occurred under the influence of the natural stimuli, and for whom electric stimulation is nothing but a physiological artefact. In fact, natural stimulation of the receptors represents a definite, biologically meaningful, pattern, whereas electrical stimulation of a nerve is biologically meaningless. It may be thought a priori that the former method of the study of afferent systems is more reasonable than the second one, particularly if the patterns of stimulation of receptive organs imitate as closely as possible those patterns which occur in the natural life of an animal.

While this rather obvious principle has been accepted for a long time by ethologists, it penetrates very slowly into the minds of neurophysio-logists. However, the first attempts to take this principle into account have appeared to be exceedingly fruitful and they seem to open large horizons for future research. Therefore, as a point of departure of the present discussion we shall consider one of these attempts, which seems to be particularly instructive, namely that represented by a series of studies recently performed on the visual afferent system by H u b e l and Wiesel (1959, 1961, 1962, 1965).

Hubel and Wiesel have found that the higher the level in the hierarchy of the visual system, the more complex and refined the stimuli activating, in the optimum way, its units (Fig. 1). If the recording microelectrodes are placed in the lateral geniculate body of the anesthetized cat, then, according to these authors, the optimum stimuli for activation its neurons are represented by small spots (white, dark or colored) of a definite diameter. When the responses are recorded from the neurons of the

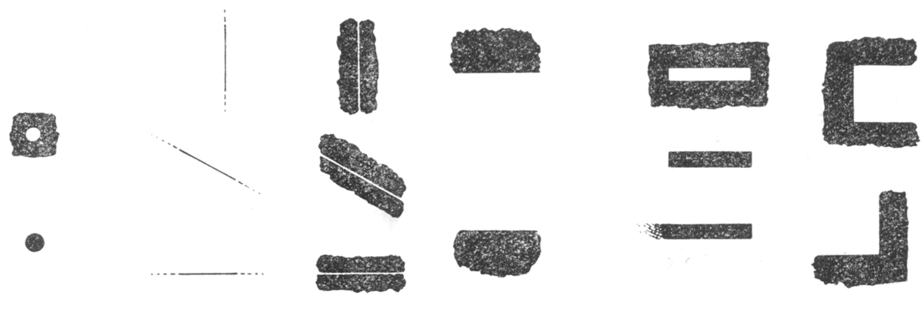

Fig. 1. The adequate stimuli for activating the units of the lateral geniculate body (left), projective visual cortex (middle) and paraprojective visual cortex (right)

striate cortex, adequate stimuli are provided by straight lines of indefinite length but of quite definite orientations from horizontal to vertical. They are of three kinds, namely dark bars against the light background, light bars against the dark background (slits), and edges separating dark and light planes. Now if we proceed to the visual fields of still higher orders, the so called para- and peri-striate cortex, we see that the units located

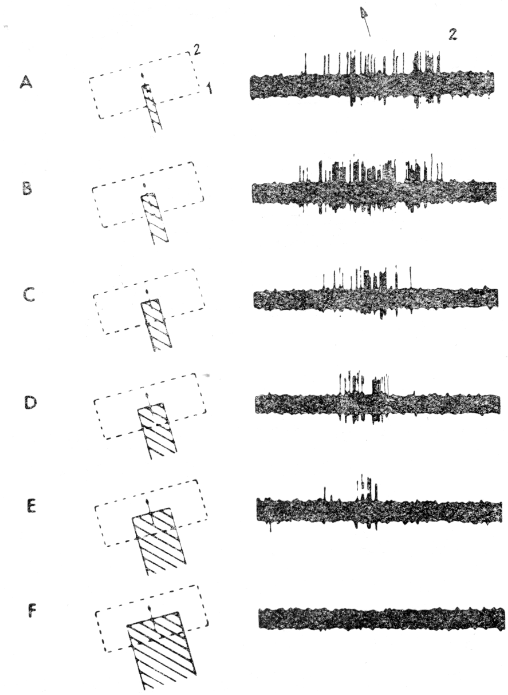

Fig. 2. The responses of a unit in paraprojective visual area to "tongues" of various width and slightly oblique direction. On the left "tongues" moving upwards in the receptive field, on the right the responses of the unit. Note that the most adequate stimulus-pattern is that in B (From Hubel and Wiesel, 1965)

there react to still more complex patterns, namely bidirectional edges (corners), dark or light bars of a definite width, limited on one end (tongues) or two ends (rods). Figure 2 taken from a paper of these authors illustrates this fact.

The problem arises as to how these facts can be explained? If we take into account the receptive surface, i.e. the retina, we know that it is composed of on-elements which react to the increase of illumination — or brightness, and off-elements which react to the decrease of illumination —

or darkness. (We omit for the sake of simplicity the problem of color vision.) It may be assumed that the spots of various kinds to which the units of the lateral geniculate bodies react are obtained by convergence of particular elements of the retina upon these units, for instance of on-elements in the center of the spot and off-elements on its periphery, or vice versa. By convergence of geniculate units, representing spots of the same kind distributed in one row, upon units of the cortical projective area, each of these units will represent a line of particular orientation. A combination of two lines at right angles may produce a corner, which can be represented in the afferent area of a still higher order. In this way a unit of the highest level represents a top of a pyramid whose base consists of a particular assembly of elements of the receptive surface. Since the same receptors and the same units of the lower levels take part in different combinations in various pyramids, it is clear that the number of pyramids may exceed the number of units of the lower levels. The fact that all afferent systems have indeed the convergence-divergence organization is in agreement with this notion.

II

We may easily observe that all the above specified stimulus-patterns, adequate for activating the units of particular levels of the visual afferent system, although certainly complicated from the point of view of a neurophysiologist who is concerned with their analysis, are nevertheless exceedingly simple and primitive in comparison with those patterns which a subject, whether he is a human being or an animal, actually does perceive and reacts to. In fact we perceive people, human faces, animals, small objects from nearby, large objects from afar, and we have no doubt whatsoever that cats or monkeys (which were the subjects of H u b e l and W i e s el’s experiments) have roughly the same perceptions, judging from their behavioral responses. However, neither we nor animals notice separate lines, edges, corners, "tongues" or "rods" which were the adequate stimuli for the units so far investigated. We are indeed able to pick out deliberately these elements from the whole objects seen by us, but this process is based on the analysis of the visual patterns of these objects, and not on their more primitive immediate perception. Thus, although these elements of the perceived objects certainly do exist in our (and animals') visual reception, we normally do not pay attention to them, or realize their existence.

Even more clear is the situation in respect to perceptions in other analyzers, because here their secondary analysis aiming at isolation of their elements is often totally impossible: We are not able to resolve the sound of the voice of a given person into the spectrum of its acoustic elements, although we recognize the voice without any difficulty. An illiterate person is not able to resolve the sound of a word into the phonems, and even those highly educated in linguistics cannot resolve a word spoken into its kinesthetic elements. The taste of a given dish is recognized as such without its analysis, and the same is even more true in respect to olfactory stimuli. In fact, one of the reasons of the foundation of the gestalt-psychology was the realization of the fact that our perceptions are not formed through the association of simple sensations, as was claimed by associationistic psychology of the 19th century.

Now the crucial problem arises as to why this is so.

It may be supposed that particular units of the so called associative areas of the cortex become interconnected in various ways forming what H e b b (1949) has called cell-assemblies corresponding to particular perceptions. These connections, according to his theory, are so well established and multi-directional that it is enough to put intoaction one unit in order to activate the whole assembly.

However, having at our disposal the recent data obtained in Hubel and Wiesel's experiments we can extrapolate them and explain the origin of perceptions by the same principles as were found to operate on the so far examined levels of the afferent systems. In other words, we can suppose that single perceptions, such as are experienced in human and animal life, are represented not by the assemblies of units, but by single units in the still higher levels of particular afferent systems. These units are formed by integration of elements represented in the units of the immediately preceding level in the same way as the latter ones were formed by integration of elements of the lower levels. We shall call these highest levels of afferent systems gnostic areas, and the units responsible for particular perceptions will be called gnostic units. We shall try to show that by this hypothesis many facts in the field of perceptive processes can be satisfactorily explained.

Before entering into this discussion one should notice that there is an essential difference between the units of all the afferent areas dealt with so far, and the units of the gnostic areas. The role of the former units which we propose to call transit units consists in integrating the elements of receptions into more and more complicated patterns constituting the raw material for the gnostic units of the highest level of each afferent system. These latter units may be also called exit units, because their role is to utilize the stimulus-patterns integrated in the given afferent system for association with gnostic units of other afferent systems, and in particular for the behavioral acts (Fig. 3).

One important inference follows from this analysis. This is that once the task of a given transit afferent field is fulfilled, i.e. this field has handed over the stimulus-patterns represented in its units to the afferent field of the higher order, these stimulus-patterns do not participate any more as separate items in the further information processing, since the; are amalgamated into one whole and thus completely lose their individuality. A unit of the higher order representing some integrated stimulus-pattern does not "know" from which components it is synthetized. Thus, we come to the solution of the vexing antynomy contained in the

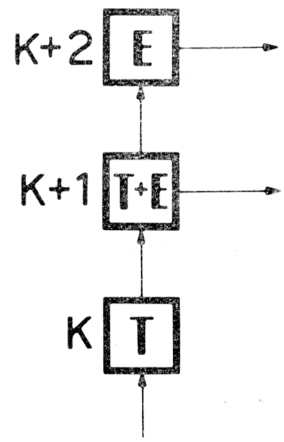

Fig. 3. A schema of transit (T), transit-exit (T+E) and exit (E) afferent fields
K, K + 1, K + 2, consecutive levels of the afferent systems, perpendicular arrows, transit connections, horizontal arrows, exit connections. Note that the level *K + 1* has both transit and exit units. The latter ones belong to the lower reflex-arcs originating from visual receptors

gestalt-psychology, according to which on the one hand, the perceptions are certainly composed of the simple elements provided by particular receptors of the given receptive surface, but on the other hand these elements are totally lost in our perceptions, since we do not realize at all which elements they are made up of. Even if we do perceive some simple patterns, represented in the lower level of the given afferent system, such as lines or edges in the visual analyzer, or pure tones in the auditory analyzer, it is not because we utilize the corresponding units of the lower levels, but because we form the special gnostic units in the highest level; in other words, the simplicity of these perceptions is only apparent, and they are, in fact, even more sophisticated than our usual perceptions because they do not belong to the natural repertory of our perceptive experiences.

It should be added that the more developed the given afferent system, and the more complex the stimulus-patterns represented in its gnostic units, the higher the ladder of transit areas which mediates the final result. The same principle certainly operates in phylogeny: the more developed the brain of a given species, the more levels the particular afferent system possesses. This is why, as is well known, the development of the cerebral cortex is accomplished not by the extension of the primary projective areas, which remain strikingly constant in various species, but by the superimposing upon them (in the functional sense) of new levels of cortical integration.

Unfortunately we have now no direct electrophysiological evidence to show that perceptions are really represented in units of gnostic areas, and therefore we ought to present as much as possible indirect material suggesting that this is so. This material comes chiefly from psychological considerations, and from neuro-anatomical and neuropathological evidence. We shall survey briefly all these sources of information.

III

Right at the beginning of our analysis it should be emphasized that we shall be concerned here with only one form of perceptions, namely that occurring by paying attention to a definite, already known stimulus-object and recognizing it at once without any special examination. The typical examples of such phenomena are: recognizing a familiar face or an object of everyday use immediately after looking at it, the voice of a familiar person after hearing only one word, the known taste of a food placed on the tongue, the known smell, the position of the limb, when we pay attention to it, etc. We shall call such perceptions unitary perceptions in contradistinction to complex perceptions which occur when we scrutinize a given object by shifting our attention from one of its elements to another.

It is clear that the unitary perception, according to this definition, can be experienced when, and only when, the appropriate gnostic unit (or rather a number of equivalent units as we shall see later) is already formed in a gnostic area of a given afferent system. Thus gnostic areas may be considered as files of gnostic units representing all unitary perceptions established in a given subject.

Let us turn now to the analysis of the chief psychological properties of unitary perceptions in order to see how these properties fit into our hypothesis concerning their anatomical and physiological basis.

1) The first property, already mentioned before, is the integrity of unitary perceptions, that is that they occur at once as single mental events. There are some rare cases when a given stimulus-object seems to us dubious, i.e. we hesitate as to which category it should be classified to, but even then the alternatives do not mix, but rather follow one another in quick succession as is the case in the ambiguous figures well known in psychological testing. In some other cases we do not recognize a stimulus-object at the first glance because it is entangled with other patterns; this may happen when the visual object is presented against

a patchy background, or a familiar sound is heard in a noisy environment. But, again, if after some delay the stimulus is recognized this occurs as an immediate experience and the pattern is grasped as a whole.

2) Another important feature of unitary perceptions is the complementary character of their elements. As follows from our concept, the elements which a given unitary perception is composed of mutually complement each other because the units of the lower level representing those elements converge upon the corresponding gnostic unit. This is best shown by the fact that if one element of a given stimulus-pattern is missing, or replaced by a different one, or a new element is added (which means that off-elements are replaced by on-elements), then one of two things may happen. Either the change will not be noticed at all, that is the presented pattern will be accepted by the corresponding gnostic unit in spite of its small alteration, or the deformation of the pattern will be enough to totally prevent its recognition. In that case the pattern will not be acknowledged as belonging to our perceptive file, but considered as quite a new pattern.

There are many examples from our everyday life illustrating this principle. On the one hand, we often fail to recognize a familiar face in new headgear, or when a beard is added or removed, spectacles worn or not. Similarly we fail to recognize the sound of a word if only one phonem is changed, or subtracted, or added. On the other hand, it often happens that when reading words we do not notice an omission or change of a letter, an experience familiar to everybody who reads proofs.

It may also happen that an object is recognized, but it is found that "something" is changed in it. This occurs when, owing to a corresponding association, we are expecting a given stimulus-object, and not another one, in a given situation. A typical case is when we see a well known person with some change of dress. The failure of realizing at once what has changed in the appearance of the person again clearly shows that the particular elements do not participate as such in our perception.

3) The next property of unitary perceptions is the relevance of particular elements and irrelevance of others. It is easy to observe that not all elements of a stimulus-object projected on the receptive surface are necessary for its recognition. In fact the sketch of a face of a given person composed of only a few lines may resemble the original so well that everybody recognizes it without any hesitation, that is the sketch certainly activates gnostic units representing that face in spite of its simplicity. These facts remind us of the well known ethological data showing that the much simplified models of a predator, or a subject of the opposite sex may easily substitute the original animal (Fig. 4). All these facts indicate that in our own perceptions, exactly as in those of

animals, there are essential elements whose lack or change destroys totally the perception, and irrelevant ones which play a minor role, or no role at all, in establishing a given gnostic unit. Which elements are essential and which irrelevant for the given unitary perception can be found only by special experimentation similar to that carried out by the ethologists.

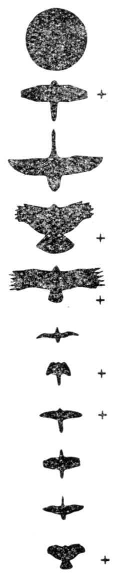

Fig. 4. Models of various birds presented to chicken
The movement of models ts from down to up. The models denoted by + release escape responses. Note that the chief characteristic of the predator is its short and thick "neck", other properties being Irrelevant. (From Tinbergen N. 1955)

The principle of selectivity of relevant elements of perceptions can be again easily deduced from our concept, and moreover it makes this concept much more conceivable. In fact, we see that a given gnostic unit does not represent an innumerable multitude of elements of the stimulus-pattern concerned. This would be simply inadmissible, because it would require an unbelievable quantity of units and their connections. Besides, this would be inadmissible from the biological point of view because too great a selectivity of gnostic units would be highly maladaptive. As a matter of fact, the integration of the afferent input consists as much of the convergence of features which are inherent in the given stimulus-object, as of sorting out those features which for some reason or another seem to be irrelevant or even misleading.

4) The distortive or rather corrective character is another general feature of unitary perceptions. Already on the level of transit afferent fields there is a distortion of the exact copy of a stimulus-pattern

produced by exacerbation of contours due to the interplay of on- and off-units and their more or less prompt adaptation. This distortion is strongly increased when we move to the gnostic areas. This is particularly evident in the visual analyzer. In fact, gnostic units do not reproduce faithfully the size of the visual stimulus-object, such as is projected on the retina, but correct it according to its standard (the so called principle of constancy). This is why looking at a television screen we perceive normal sized people and not dwarfs, and we perceive a tree in front of our window to be much larger than the flowers on our table, although the angular size of the latter may be even greater than that of the tree. Similarly, our wrist-watch seems to us nearly always round, although its retinal projection is most often oval. All these distortions of visual patterns projected onto the retina, which are described in detail in psychological textbooks, are explained by assuming that a gnostic unit represents a standard for the given stimulus-object, and therefore it bends the actual reception to this standard not bothering about the photographic accuracy of the picture.

5) The next important property of unitary perceptions is their categorization. Unitary perceptions within each analyzer are divided into categories, the principle of division being based chiefly on the differences in the kinds of elements of which they are composed. To give some examples, we have in the visual analyzer separate categories of perceptions representing particular human faces, human figures, small palpable objects, letters and other signs, etc. Similarly, in the acoustic analyzer we have separate categories of perceptions representing known sounds of the environment, words, people's voices or melodies. In the somatic analyzer we can discern the category representing textures of objects touched, their shapes, etc. We shall see later that categorization of perceptions has a well expressed counterpart in the anatomical organization of the gnostic areas.

6) The last important property of unitary perceptions is their mutual antagonism. It is not possible to discuss this matter more thoroughly here, therefore we shall limit ourselves to noting that this antagonism is most strong among the unitary perceptions of the same category. This phenomenon is probably based on the principle of the so called lateral inhibition which seems to play an even greater role in the gnostic fields than in the lower levels of the afferent systems. In fact we cannot perceive simultaneously two faces, unless they form a familiar group (say, on a photograph), or two words spoken simultaneously by two persons.

On the contrary the unitary perceptions of various categories, and even more so of various afferent systems are only slightly antagonistic between each other, if at all. For instance, seeing a given person is not antagonistic to hearing his voice, nor to listening to what he says, and seeing a rose is not antagonistic to smelling its odor. Similarly, hearing the words of a song and its melody does not conflict each other.

IV

We shall turn now to a discussion of neurogical evidence of the existence of gnostic units.

First, if we look at the general anatomical organization of the cerebral cortex, we can easily notice that the so called "projective" areas and "associative" areas (our gnostic areas) have quite different intercortical connections. While the former ones (being the transit areas according to our terminology) send their axons only to the adjacent areas still belonging to the given analyzer, the latter ones, called exit areas, send their axons to various portions of the cortex through the long associative pathways. The complete congruence of this fact with our concept does not need any comment.

Even more informative are the data obtained on the basis of clinical observations of subjects with lesions in particular parts of the cerebral cortex.

There is a large body of evidence to show that lesions in the projective transit areas of the cortex produce quite different deficits in the higher nervous activity of the patients from those sustained in the gnostic areas.

Lesions in the projective cortical areas give rise to defects in the sensations of the given modality of stimuli. These defects have as a rule a clearly topical character provided that the lesion is not too extensive. For instance, after lesions in the somatic area the tactile and joint sensitivity of a particular part of the body contralateral to the lesion is impaired, i.e. the feeling of touch is blunted, and the patient fails to apprehend the position of his limb. After lesions in the visual area the chief symptom is hemianopia whose localization depends again on the site of the injury. One can assume that in both cases a part of the cortical transit units of the given analyzer is destroyed, and therefore the messages from the corresponding receptive surface cannot reach the gnostic area.

Quite different is the symptomatology of lesions sustained in the gnostic areas. Sensation as such is usually unimpaired, however the patient displays peculiar defects, which are referred to as agnosias.

Thus a patient with some occipital damage may be unable to discern and recognize human faces (the symptom denoted as prosopagnosia) even of his close acquaintances, although he perfectly recognizes other visual object which may even provide him with a cue for recognizing a given face. Other patients have no difficulty in recognizing faces but have great trouble in recognizing the manipulative objects of common usage. They are able, however, to recognize them immediately after taking them in the hand. Still other patients manifest a selective loss of recognizing letters and other signs (alexic agnosia). A patient with a lesion in the left temporal region cannot grasp the sound of words, although he is perfectly able to recognize all other sounds ("word deafness"). The opposite defect of not recognizing all sounds except words was also reported after lesion in the right temporal region. A patient with parietal lesion fails to perceive the shape of objects, although his tactile sensation may be unimpaired (astereognosia). Finally, there are patients who can perform all the movements of their mouth involved in eating, showing a good oral kinesthesis but fail to produce words, having lost the necessary kinesthetic patterns involved in verbalization (Broca aphasia). Thus, particular lesions in the gnostic areas do not destroy the receptions of the corresponding stimuli, but destroy the perceptions of particular categories of stimulus-objects.

In this way we come to the important conclusion that while the units of the transit areas of afferent systems are chiefly arranged according to the topographic principle, each area being a projection (in a geometrical sense) of the receptive surface, the units of the gnostic areas are arranged by a clustering of those units which represent the same categories of stimulus-objects. It seems that the categorization of stimulus-objects of each analyzer is chiefly based on the types of elements they are composed of, and on the types of associations which they form with other afferent systems.

V

It is not possible for us within the limits of this article to discuss in detail the next important problem concerning the formation of gnostic units when the new meaningful combination of receptive elements impinges upon the receptive surface. To put it short, we assume that between the lower levels of afferent systems and the gnostic areas potential connections exist based on not fully developed synaptic contacts (cf. Konorski 1948). These potential connections are transformed into actual connections when a new stimulus-pattern is presented in a state of "receptiveness" of the corresponding afferent system produced by its unspecific activation, that is, when a subject pays attention to a given modality of stimuli. We further assume that a given stimulus-pattern is represented in the appropriate gnostic field by a set of equivalent units (rather than by a single unit), their number depending, among other things, on how early in life the perception of that pattern was acquired.

This assumption explains the fact that in diffused encephalopaties, in which the cortical neurons are decimated, the old memory traces are better preserved than those acquired later.

When the two stimulus-patterns repeatedly presented to the subject do not differ in their essential elements, they are represented by the same set of gnostic units, i.e. they are indistinguishable. If, however, each of them has a different physiological significance, and therefore, they have to be discriminated, then two new sets of gnostic units are formed, each of them representing not only the crude aspects of the similar patterns but also their specific characteristic. Thus the process of discrimination of similar patterns is explained by assuming that each of these patterns is represented both by gnostic units corresponding only to their common features and those corresponding to their specific traits (Fig. 5).

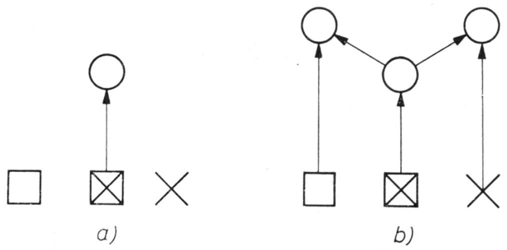

Fig. 5. A diagram of the process of discrimination of two similar stimulus-pattern
a, before discrimination, b, after discrimination. The elements constituting one pattern are denoted by squares, the other one, by crosses, gnostic units by circles. In a gnostic units are formed only to the common elements of two patterns and therefore they are indistinguishable. In b new gnostic units are formed representing both the common and the specific elements of the two patterns

If two known stimulus-patterns of the same or different afferent s are synchroneously presented under a state of unspecific receptiveness of these systems, then the association between these patterns is formed, based on the formation of actual connections between their gnostic units. The prerequisite of this association is the existence of potential connections, or anatomical pathways, linking the gnostic fields concerned. The connections are, of course, always unilateral, therefore, the bilateral associations are based on separate connections linking the sets of units in both directions.

The phenomenon of classical conditioning is nothing else but the association between two stimulus-patterns of which one is "labeled" by producing an over unconditioned response. If the first of the two paired stimulus-patterns starts to evoke the same response, this is the objective sign that the actual connection between the corresponding sets of gnostic units are formed.

To summarize, the problem we have considered was how the flow of information provided to the higher organisms from the external world is handled by the nervous system. Taking into account the substrate on which this handling takes place, a substrate composed of billions of nerve-cells, and fibers along which the nerve impulses travel from one cell to another, two different hypotheses of the mechanisms of this handling are conceivable. One hypothesis, which may be called modulation hypothesis is that the temporal patterns of impulses conducted by the same fibers give rise to the variety of information conveyed by them, a mechanism somewhat similar to that used in typical, old-fashioned wire telegraphy using the Morse coding. The other hypothesis which may be called topographical hypothesis, claims that it is not the sequences of impulses that matter in conveying particular messages, but rather the units to which they are addressed.

It is clear that in this paper a topographical theory of perceptive processes was advanced, which *ipso facto* means a discarding of the modulation theory. Indeed, we think that although the modulation hypothesis seems to be supported by some experimental findings showing different changes in rhythms of brain activity and action potentials produced by different stimuli, it cannot serve as an explanatory principle of the perceptive and associative processes; for this hypothesis becomes useless as soon as we go beyond these experimental findings and take into consideration not the artificially simplified and unnatural signals, but actually occurring stimulus-objects impinging upon our receptors. In fact, as we tried to emphasize in this discussion, the main features of perceptual processes are their numerousness, and their distinctiveness and we do not think that these two features can be reliably conveyed by different temporal groupings of impulses along the same channels or pathways. Perhaps we cannot help using such a method when we have a cable composed of a limited number of lines as is the case in wire telegraphy. If, however, we have at our disposal billions of lines and addresses, as is precisely the case in the central nervous system, and if the number of these lines and addresses increases pari passu with the phylogenetical development of the brain and the increasing amount of information utilized by it, then to recur to the complicated methods of "coding" that information by temporal sequences of impulses would seem to be unthinkable.

REFERENCES

HEBB D. 0. 1949—The organization of behavior. A neuropsychological theory. New York: John Wiley and Sons.

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

HUBEL D. H. and WIESEL T. N. 1961 — Integrative action in the cat's lateral geniculate body. J. Physiol. Lond., *155, 385.*

HUBEL D. H. and WIESEL T. N. 1962 — Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol., Lond. 1*60*, 106.

HUBEL D. H. and WIESEL T. N. 1965—Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. J. Neurophysiol., *28*, 229.

KONORSKI J. 1948 — Conditioned reflexes and neuron organization. Cambridge: Cambridge University Press. TINBERGEN N. 1955—The study of instincts. Oxford: Clarendon Press.