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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

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* 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 neurophysiologists. 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 Hubel 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 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.

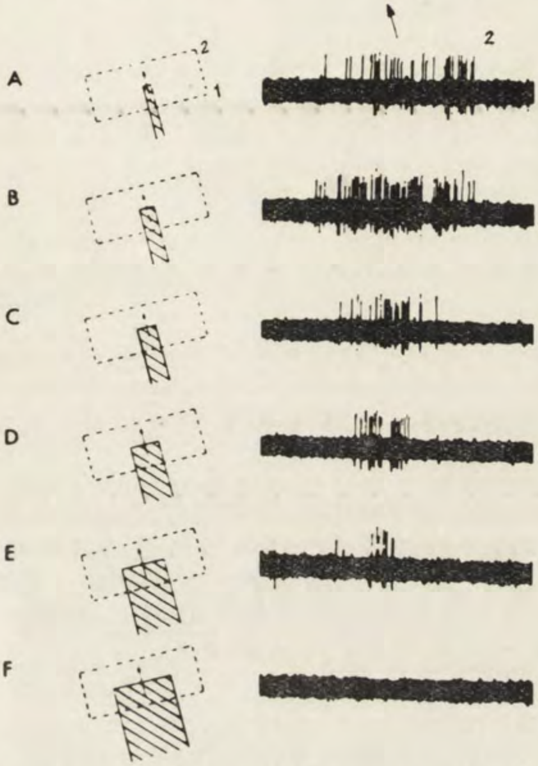

Fig. 2. The responses of a unit in paraprojective visual area to "tongues" of various width and slightly oblique direction. On the left "tongues" moving upwards in the receptive field, on the right the responses of the unit. Note that the most adequate stimulus-pattern is that in B (From Hubel and Wiesel,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

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 Hubel and Wiesel'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 Hebb (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 they 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 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.

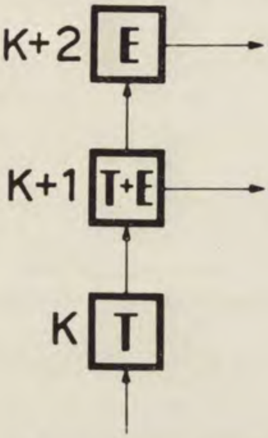

Fig. 3. A schema of transit (T), transit-exit (T+E) and exit (E) afferent fields

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

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 is 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 objects, 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).

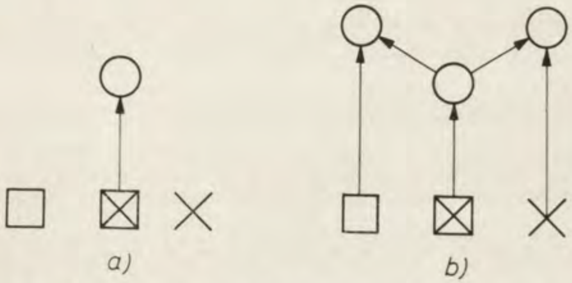

Fig. 5. A diagram of the process of discrimination of two similar stimulus-pattern

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 systems 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 given 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 rythms 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.

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QUALITATIVE VERSUS DIRECTIONAL CUES IN DIFFERENTIAL CONDITIONING

I. LEFT LEG-RIGHT LEG DIFFERENTIATION TO CUES OF A MIXED CHARACTER*

Czesława **DOBRZECKA** and J. **KONORSKI**

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

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In a recent study of Ławicka (1964) the dogs were trained in two differentiation tasks either to two tone frequencies or to two directions of the same tone. It has been found that if the animal is trained in go left-go right differentiation, the task is easily solved when a tone of the same frequency is presented from below or above respectively, but is very difficult when two tones of different frequencies are presented from the same place. On the contrary, when the animal is trained in go-no go differentiation, the task is very easy with two tone frequencies, but it is difficult when the same tone is presented from different places. In other words, depending on the tasks with which the animal is confronted — go left-go right versus go-no go differentiation — directional or qualitative cues are adequate respectively for its solution.

In Ławicka's experimental set up, the differentiated instrumental responses consisted in approaching one of the two feeders situated on the left and on the right side of the starting platform. Therefore, the problem arose as to whether the same principle, as that found by Ławicka, is in operation when the animal is trained to perform two manipulatory (not locomotor) instrumental acts and the food is presented in the same feeder. The present study deals with this problem. A preliminary report of these experiments was presented elsewhere (Dobrzecka et al. 1966).

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MATERIAL AND METHOD

Experiments were performed on 11 dogs in a regular soundproof CR chamber. Two stimuli were used as CSs: the sound of bubbling water and the sound of a metronome. The device producing bubbling was located on the floor behind the stand, whereas the metronome was located in front of the animal at head level.

The dogs were trained to raise their right fore legs and place them on the feeder in response to the metronome (MA) and to raise their left fore legs and place them on the feeder in response to the sound of bubbling (BP). Each correct movement was reinforced by moving into position a bowl with bread moisted by broth. Eight or nine reinforced trials were given in each session with intervals of about 1 min.

The training procedure consisted of the following stages. At the beginning, a technician stood before the animal holding two strings attached to bands around the wrist of each fore leg. The experimenter sitting in the prechamber put into action either the metronome or the bubbling in random order. After 5 sec the appropriate fore leg was passively placed on the feeder by the technician and then immediately the bowl with food was put into position.

After several experimental sessions the dog started to perform occasionally the trained movements actively, within 5 sec of operation of the CS. When the movement was correct the food was immediately presented, when it was wrong food was not given and the CS was discontinued. If during 5 sec no movement was performed the appropriate leg was lifted by the technician and this was reinforced by food.

Finally, the animals learned to perform active movements to each presentation of the CS. In this period the dogs were left in the chamber alone and the following procedure was adopted: when the animal performed the correct movement the food was immediately presented; when he performed the wrong movement the stimulus was discontinued and food was not given.

After a criterion of not less than ten consecutive errorless sessions was reached, a series of ten test sessions was given. Each session began with two or three regular trials after which a CS operating from the place of the other CS was given (e.g. a second metronome placed behind). This was followed by two or three regular trials succeeded by the other CS operating from the reverse position (e.g. another apparatus for bubbling placed in front). Some examples of regular and test sessions are presented:

Regular sessions

MA, BP, BP, MA, BP, MA, MA, BP
BP, MA, BP, MA, MA, BP, BP, MA

Test sessions

MA, BP, *MP*, MA, MA, BP, *BA*, BP
BP, BP, MA, *BA*, MA, MA, *MP*, BP

MP means the metronome sounding from behind, BA means the bubbling sound from in front. No matter what movement was performed by the animal in a test trial food was offered. If no movement was performed food was not presented.

RESULTS

The course of training is represented in Table I for all dogs except two in which the procedure was not quite typical. In the first stage of training, which included in average 25 trials, only passive movements were present. Thereafter, among the trials with passive movements, in some trials the animals started to perform active movements (correct or otherwise). Eventually the dogs performed correct active movements in all trials with a latency not exceeding one or two seconds.

After the differentiation had been established, the dogs behaved in each session in a stereotyped manner: in response to the metronome they looked to the fore and then performed the movement of the right leg, whereas in response to bubbling they turned backward, and performed the movement of the left fore leg. Some of the dogs were sitting in a "neutral" position with the head turned to the side wall, so as to be in a position to quickly turn the head to the right (i.e. behind) or left (i.e. to the front).

Table I

The course of right leg-left leg differentiation to MA and BP

Dog	Passive movements till first active movement		Total number of passive movements		Total number of errors		The number of trials till criterion
	M A	B P	M A	B P	M A	B P	
1	8	8	24	18	7	13	160
2	5	3	10	9	10	11	280
3			10	14	7	10	120
4	49	57	77	70	12	16	280
5	17	23	18	24	7	4	200
6	35	22	41	33	8	6	360
7	10	20	18	21	4	8	160
8	27	24	30	24	8	3	160
11	27	25	75	32	5	15	360
Average	22,2	22,8	33,7	27,2	7,6	9,6	231,1

The responses of the animals to the CSs sounding from the reverse position are presented in Table II. It is seen that most animals reacted to the position of the stimuli and not to the quality. This means that bubbling placed in front of the animal elicited in most instances the movement of the right fore leg, whereas the metronome placed behind elicited the movement of the left fore leg. Only three dogs did not react consistently according to these rules.

Dog No. 2 in the first series of test sessions reacted to bubbling placed in front of him according to the quality of the CS, whereas to the metronome placed behind he reacted mostly according to the direction of the stimulus. In consequence he raised to both test stimuli the left fore leg. Since the animal became restless during the test sessions and committed errors even in regular trials, additional regular training was given, and then the test series was repeated. This time the dog reacted consistently according to the direction of both stimuli.

Table II

Test trials in right leg-left leg differentiation originally trained with MA and BP respectively

Dog	Response to MP according to:			Response to BA according to:		
	quality (M)	direction (P)	no response	quality (B)	direction (A)	no response
1	0	9	1	0	10	0
2(a)	2	8	0	10	0	0
2(b)	0	10	0	0	10	0
3	1	8	1	0	10	0
4	0	10	0	0	10	0
5	0	10	0	1	9	0
6	0	10	0	0	10	0
7	0	10	0	2	8	0
8	5	5	0	1	9	0
9	2	8	0	2	8	0
10	0	10	0	0	10	0
11	4	1	5	0	10	0
Average percentage	11,7	82,5	5,8	13,3	86,7	0

(a) First series of test sessions in dog No 2.
(b) Second series of test sessions in dog Nr 2 after additional training.

Dog No. 11 reacted to bubbling from the front according to the direction of the stimulus (i.e. raised the right leg), whereas he displayed a strong orientation reaction to the metronome placed at the back, and either performed no movement at all, or reluctantly reacted according to the quality of the CS (i.e. also raised the right fore leg). Dog No. 8 gave mixed responses to the metronome situated behind.

In some dogs shifting the stimuli produced a manifest orientation reaction of the type "what is it?": the animals gazed attentively to the stimulus situated in the not usual place, and the conditioned response was slightly delayed or even absent. This orientation reaction was, however, transient and after a few test trials it disappeared.

DISCUSSION

It is clear from our experimental findings that when the dogs were confronted with the task of left leg-right leg differentiation, the solution of which could be based on either the directional cue or the quality cue, they regularly chose the former cue and virtually completely neglected the latter. This result is particularly impressive in view of the fact that the qualities of the two stimuli used in our experiments (the sound of a metronome and that of bubbling water) have nothing in common and hardly any generalisation is observed between them. Thus, the results obtained earlier by Ławicka in experiments with locomotor responses leading to two different feeders have been fully confirmed in our experiments using manipulatory responses and a single food-well.

The explanation of these results is possible on the basis of Konorski's concept concerning the formation of conditioned intercentral connections (Konorski 1948, 1967). According to this concept the prerequisite of the formation of actual conditioned connections between two centers is the existence of inborn, potential connections (pathways) linking these centers. Thus, the formation of an instrumental CR to the quality of an auditory CS requires the existence of potential connections linking directly the units of the auditory analyzer representing that stimulus with the units of the kinesthetic analyzer representing the instrumental motor act. On the other hand, the formation of the instrumental CR to the direction of an auditory CS requires the existence of potential connections between the kinesthetic units representing the appropriate orienting reaction and the kinesthetic units of the instrumental act. Ławicka's and our experimental results show that in dogs the latter connections are more potent than the former ones. In consequence, when the formation of both types of connections is available in the given conditioning procedure, the kinesthetic-kinesthetic connections take the upper hand over the auditory-kinesthetic connections (cf. Konorski 1964, Fig. 7).

The probleme arose as to how to explain those cases in which the animals behaved against the rule of the dominance of directional cues over quality ones. It should be noted that none of our dogs behaved consistently according to the quality cue, but did so apparently only in respect to one stimulus. Since in these dogs the changed position of stimuli produced a strong disturbance of the conditioned responses even in the regular trials, it may be assumed that the animals simply developed a preponderance of responding with one leg to both stimuli; in fact, we do know that such type of perseverative behavior may occur at the beginning of training, or when an animal is upset. In consequence, we do not think that in these exceptional cases the animals really followed the qualitative aspect of the CS, but rather they displayed a dominance of one response over the other. This conclusion is supported by the results of the next study in which both CSs were situated in front of the chamber and the animals had to base their responses exclusively on the qualitative cues.

SUMMARY

1. Eleven dogs were trained in left leg-right leg differentiation to two CSs which differed both in quality (bubbling versus beats of a metronome) and direction (behind the animal and in front of the animal). After the task had been mastered 20 test trials were given in which the positions of the CSs were reversed.

2. Eight dogs reacted in all, or almost all, instances to the direction of a tested CS, totally neglecting its quality. Two dogs reacted to the direction of one stimulus but apparently according to the quality of the other one, whereas one dog displayed mixed responses. After repetition of the regular training one of these dogs reacted in test trials only to the direction of the CS.

3. The possible physiological mechanism of the results obtained is discussed.

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QUALITATIVE VERSUS DIRECTIONAL CUES IN DIFFERENTIAL CONDITIONING

II. GO-NO GO DIFFERENTIATION TO CUES OF A MIXED CHARACTER*

Genowefa SZWEJKOWSKA

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

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In the experiments of Ławicka (1964) it was shown that whereas the task of the go-no go differentiation is much easier to tone frequency cues than to directional ones, the reverse is true in respect to the go left-go right differentiation: here the task is very difficult when two tones of different frequencies are used, but it is quite easy when the same tone operates from two different places.

In the present series of experiments the problem of the significance of cues for the two types of differentiation, has been resumed under different experimental procedure than that used in Ławicka's study: first, manipulatory instrumental responses were used instead of locomotor responses; secondly, the animal was provided with both directional and qualitative cues in the same experimental procedure, and had to select that cue which was most suitable for him in a given task.

In the preceding paper of this series (Dobrzecka and Konorski 1967) it was shown that in the left leg-right leg procedure the dogs solved the differentiation problem almost completely on the basis of directional cues neglecting the qualitative cues. The present paper is concerned with an analysis of the go-no go differentiation task. A preliminary report of these experiments was published elsewhere (Dobrzecka et al. 1966).

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MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were performed on ten dogs in a regular soundproof CR chamber. In the first stage of training, the animals were taught to lift the right foreleg and place it on the feeder in response to the auditory CS for food reinforcement. The method of passive movements was used (see Dobrzecka and Konorski 1967).

In six dogs belonging to group I the CS was a buzzer (B); in three dogs it was situated in front of the animal (BA) and in three other dogs behind (BP). In four dogs belonging to group II the CS was a tone of 900 cycle/sec (T_1): in experiments with two dogs it was situated in front (T_1A) and in two behind the animal (T_1P). Intertrial intervals were 1 min.

Table I

Schedule of experiments

Dogs	CS+	Its location	CS−	Its location
		Group I		
1	BA	In front	MP	Behind
2	BA	In front	MP	Behind
3	BA	In front	MP	Behind
4	BP	Behind	MA	In front
5	BP	Behind	MA	In front
6	BP	Behind	MA	In front
		Group II		
7	T_1A	In front	T_2P	Behind
8	T_1A	In front	T_2P	Behind
9	T_1P	Behind	T_2A	In front
10	T_1P	Behind	T_2A	In front

When the animals performed the trained movements in hundred per cent of trials and the intertrial movements disappeared, negative CRs were introduced which were never reinforced by food. For animals belonging to group I the negative CS was a metronome (M) placed in the opposite position to the buzzer: in those dogs in which the buzzer was in front the metronome was behind (MP) and in those in which the buzzer was behind the metronome was in front (MA). For animals belonging to group II a tone of 600 cycle/sec (T_2) was negative CS and was placed behind (T_2P) or in front (T_2A) depending on whether the positive CS was before or behind the animal. The positive and negative CSs for each dog are presented in Table I.

In each session 8 positive and 8 negative trials were given with intertrial intervals of 1 min. In the positive trials the dog obtained food immediately after the trained movement was performed. In the negative trials the CS lasted for 5 sec regardless of whether the animal did or did not perform the trained movement.

After the positive and negative CRs were firmly established the following test experiments were performed: in each session among regular trials two test trials were given in which once the positive and once the negative CS was sounded from the place of its antagonist. The tested stimuli were presented for 5 sec and were never reinforced by food, irrespectively of whether the animal did or did not perform the trained movement. Ten such sessions were given for each dog including 20 test trials (10 for the positive CS and 10 for the negative CS).

RESULTS

The course of training, before the test series, is represented in Table II. Looking at the number of errors in the negative trials (i.e. positive responses to the unreinforced CSs) it is seen that whereas in group I there was nearly no generalisation between the positive and negative CSs, in group II the generalisation was considerable and the negative training required about 40 trials until an errorless performance was achieved. This result is as expected in view of the greater similarity between T_1 and T_2 than between B and M.

Table II

The course of training before the test trials

Dogs	Number of trials	Number of errors in percent		Number of errors in the last 100 trials	
		positive	negative	positive	negative
Group I					
1	160	1.7	0.8	1	0
2	160	2.5	7.5	0	1
3	160	0.8	0	0	0
4	160	0	0	0	0
5	160	0	9	0	2
6	160	0	0	0	0
Group II					
7	184	10	23	5	2
8	160	0.6	17	0	4
9	160	1.2	16	0	3
10	184	3.8	20	0	7

The results of the test experiments are presented in Table III. As far as the responses to the positive CSs are concerned the results are somewhat miscelaneous. In 5 dogs (Nos. 3, 5, 7, 9, 10) the positive CSs preserved totally, or nearly totally their positive character when placed in the negative place in spite of the fact that they were never reinforced in that condition. In four dogs (Nos. 2, 4, 6, 8) the responses to the CSs were mixed with a preponderance of quality or direction. In one dog (No. 1) the CS shifted to the negative place behave consistently as a negative CS.

Table III

Test trials in go-no go differentiation

No. of dog	CS+	Reverse location	Positive responses (according to quality)	Negative responses (according to direction)	CS−	Reverse location	Negative responses (according to quality)	Positive responses (according to direction)
1	BA	BP	0	10	MP	MA	9	1
2	BA	BP	3	7	MP	MA	10	0
3	BA	BP	9	1	MP	MA	10	0
4	BP	BA	4	6	MA	MP	10	0
5	BP	BA	10	0	MA	MP	10	0
6	BP	BA	7	3	MA	MP	10	0
7	T_1A	T_1P	9	1	T_2P	T_2A	10	0
8	T_1A	T_1P	8	2	T_2P	T_2A	0	10
9	T_1P	T_1A	10	0	T_2A	T_2P	10	0
10	T_1P	T_1A	10	0	T_2A	T_2P	10	0
			70%	30%			89%	11%

More uniform were the responses to the negative CSs put in the place of the positive CSs: in all dogs but one these responses were purely negative (or nearly so), i.e. the animals reacted to the quality of the CSs, but not to their position. Only in one dog (No. 8) in which the negative CS (T_2P) was shifted from the posterior to the anterior position the responses to this stimulus were consistently positive.

To sum up, in the majority of test trials (in total 159 versus 41) the animals reacted according to the quality of the CS and not according to the direction from which it was operating (Fig. 1). In those cases in which the animal reacted to the directional cue instead of the qualitative one, this response was displayed either to the positive CS (in dogs Nos. 1, 2 and 4) or to the negative CS (in dog No. 8). No dog reacted consistently to direction of both the positive and negative CSs.

DISCUSSION

In the preceding report of this series (Dobrzecka and Konorski 1967) it was shown that in the left leg-right leg differentiation established to mixed, qualitative-directional cues the animals solved the task mainly, or perhaps even exclusively, on the basis of directional cues with total neglect of the qualitative ones. The present results show that if the animals are confronted with the go-no go differentiation, in which one

CS is reinforced by food and the other not, then in the majority of instances the quality of the stimuli determines their responses, i.e. the stimuli preserve their positive or negative meaning irrespective of the place from which they are coming.

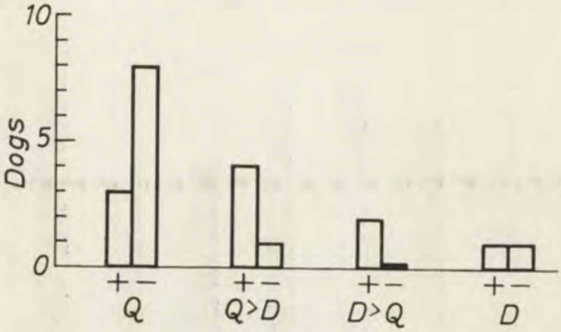

Fig. 1. Effect of reverse location of CSs on differential conditioned reflexes in go-no go differentiation

Q, number of dogs reacting only to qualitative cue; Q > D, number of dogs in which reaction to quality prevailed over reactions to direction; D > Q, number of dogs in which reaction to direction prevailed over quality; D, number of dogs reacting only to directional cues. +, reactions to positive CS (B or T_1); −, reaction to negative CS (M or T_2). The figure was drawn according to the data presented in Table III

The question arises as to why in the go-no go differentiation task domination of stimulus quality over stimulus direction is much better manifested in negative than in positive CSs. In fact, in all dogs except one the negative CSs placed in the position of the positive CSs consistently evoked negative responses, whereas the responses to the positive CSs were much more variable. At least two factors may contribute to this.

First, it should be remembered that according to our method of testing, the test trials were never reinforced. This procedure was adopted in view of the fact that, in general, reinforcement more readily leads to the formation of the positive CR than non-reinforcement leads to its extinction. Neverthless, if the animal did perform the trained movement in response to the given CS, its repeated nonreinforcement might produce some tendency to extinction. Indeed, as shown in Fig. 2 this extinction tendency was seen in dogs Nos. 2, 3, 6, 7. In dog No. 4, on the other hand, the conditioned responses were absent in the first test trials and appeared only in the succeeding trials. This effect was probably due to another factor, namely that of the orientation reaction elicited by the CS presented from the not usual place.

These two factors which handicapped the positive responses to the positive CSs obviously facilitated the negative responses to the negative CSs. In fact, in all dogs but one the negative CS transferred to the other place produced consistently the negative conditioned response. One dog (No. 8), however, broke this rule and consistently displayed the positive response to all presentations of the negative CS placed in the positive place. This shows that in this case the negative CR was established to the position of the CS and not to its quality.

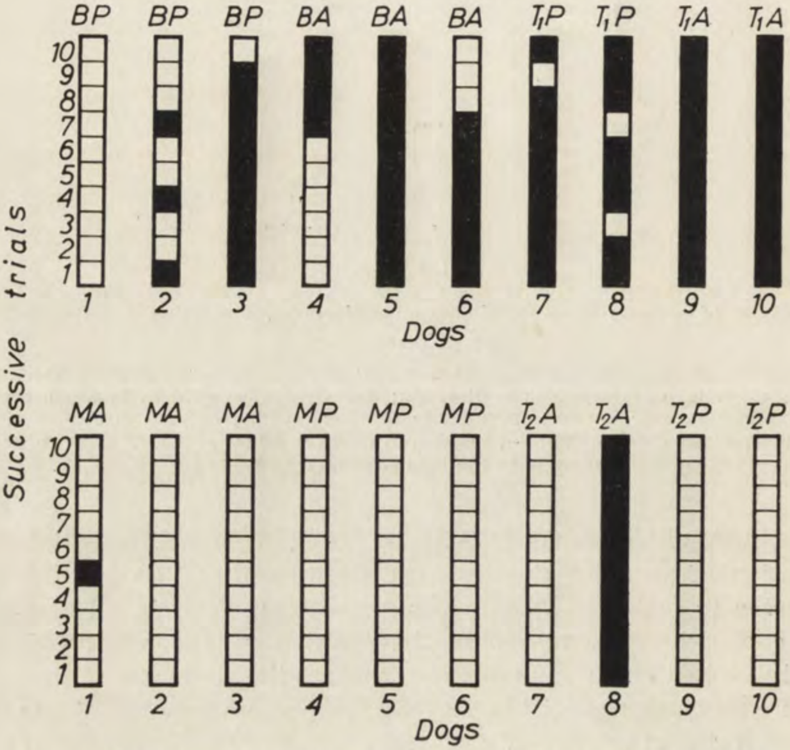

Fig. 2. Responses to quality or direction in consecutive test trials

Each column represents 10 successive test trials (from bottom to top) in each dog to positive CS (higher row) and negative CS (lower row). Black squares, positive responses, white squares, negative responses (no movements)

To sum up, it seems that on an average in the go-no go differentiation the quality cue of the CS plays a more important role than the directional cue, mainly determining the character of response. This is, however, not a general rule, because in some instances the response was exclusively or mainly determined by the direction of the CS. What is interesting in this context is the fact that in the same animal in one of the two differentiated CSs the quality cue prevailed whereas in the other one the directional cue was dominant. Thus in dog No. 1 the shift of the buzzer (positive) elicited the response congruent with its new position and not its quality, whereas the shift of the metronome (negative) elicited a response congruent with its quality. On the other hand, in dog. No. 8 the quality cue predominated in the positive CS (T_1), whereas the direction determined the response of the negative CS (T_2).

These results are only in partial agreement with the results of Ławicka (1964) in which the go-no go differentiation was virtually impossible to purely directional cues. The reason of this discrepancy in results is probably due to the fact that in Ławicka's experiments the two positions of the CSs were much less remote from each other than in our experiments. Whereas in the present study the stimuli were separated by a distance of about 2.5 meters, in Ławicka's study this distance did not exceed 80 cm. In fact, when in a later series of our experiments (unpubl.) the go-no go differentiation was trained to the same sound from before and behind, the task turned out not to be difficult and all the dogs mastered it in about 35—90 trials.

SUMMARY

1. The go-no go differentiation in manipulative CRs was established in dogs to auditory CSs differing both in quality and position in order to find out which cue is decisive in mastering the task.

2. After the shift of the positive CS to the place of the negative CS, and vice versa, the animals reacted in the majority of cases according to the quality of the CS.

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MANIFESTATIONS OF ALIMENTARY INSTRUMENTAL REACTIONS IN APHAGIC CATS WITH LESIONS OF THE ROSTRAL HYPOTHALAMUS *

Wanda WYRWICKA

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

(Received October 15, 1966)

After the discovery of a "feeding" area in the lateral hypothalamus (Brügger 1943, Anand and Brobeck 1951, Larsson 1954), a number of studies showed that some other areas located both caudally (Larsson 1954, Wyrwicka and Doty 1966) and rostrally (Brutkowski et al. 1960, 1962, Robinson and Mishkin 1962, Wyrwicka 1964) to the lateral hypothalamus are also related to food intake.

In particular, alimentary reactions quite similar to those elicited from the lateral hypothalamus could be evoked by electrical stimulation of the most rostral part of the hypothalamus (Robinson and Mishkin 1962, Wyrwicka 1964). To gather more data about the alimentary functions of this area, the present study was undertaken. This paper deals with the effects of the destruction of the rostral hypothalamus on the alimentary instrumental conditioned reactions and with a comparison of these effects to those obtained after lesions of the lateral hypothalamus.

METHODS

The experiments were performed on 18 male cats, weighting from 2.6 to 4 kg. In 8 of these cats, under Nembutal anaesthesia (40 mg/kg) stainless steel screws were placed bilaterally in the skull over the parietal and occipital cortex; these

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screws were later used as recording electrodes. In all cats a food conditioned instrumental reaction consisting in placing the forepaw on a platform located over the feeder (Fig. 1) was established. Each reaction was immediately reinforced by offering a small piece of meat. No sporadic stimuli were used. After the establishment of the conditioned reaction, 20 daily training sessions were still performed. Then, under Nembutal anaesthesia, an electrode made from wire 0·6 mm in diameter, insulated except for 1 mm at the tip, was introduced deep into the brain. In 13 cats the area of rostral hypothalamus, aimed at A 16·0, L 2 — 2·5, H — 4, and in 5 cats the area of lateral hypothalamus, aimed at A 11·0, L 3·0, H — 4, was bilaterally coagulated by means of anodal DC of 1·6 — 2 mA for 90 sec.

Fig. 1. The experimental situation. The cat is performing the trained reaction of placing its foreleg on a platforme

P, platforme, F, feeder

The cats in which aphagia developed after operation, were fed artificially; putting a little amount of hashed meat deep between the molar teeth, while the mouth was directed upwards, provoked mastication and swallowing of food. Hydration was provided by daily injections of 20—50 ml of 10% glucose solution.

Experimental sessions were resumed usually 2 days after operation. Two or three months later, the animals were sacrificed and their brains removed for the anatomical examination.

RESULTS

Cats with lesions of the rostral hypothalamus. In 8 cats of this group an aphagic state was observed for 6—16 days. The cats refused to eat any food or drink milk in their home cages, however, an occasional sniffing or even superficial licking of food was sometimes observed. In most cases the animals treated food as an indifferent object.

When these cats were taken to the experimental cage, their typical behavior was the following. A few seconds after coming to the cage, the animal performed its trained movement in the usual manner, then looked at the feeder, sometimes came to the bowl, sniffed the meat, and went away without taking any. The trained movements were then repeated several times. Initially the animal looked usually for a moment at the feeder after the performance of each movement, but later did not even turn its head towards the feeder, as if these movements were not related to any desire to eat. The intervals between the successive trained movements were irregular and the movements were less frequent than before operation. After a few minutes the animal usually stopped repeating the conditioned movement and other motor activities appeared, such as those of searching round the cage, sniffing the floor and walls of the cage, licking fur, washing themselves, etc. They seemed to ignore completely the food which was visible and accessible in the feeder. The animals looked generally excited and moved quicker than usual. No aggression, however, was observed; on the contrary, the cats were very gentle and wanted to play with the experimenter. In one cat a tendency to scratch the floor with its forepaws was observed.

The trained movements were usually most frequent in the first days after operation, then gradually disappeared. At the same time the general motor activity of the animals was still higher than, or at least similar to that of the pre-operative period.

The EEG records taken of the cats with implanted electrodes did not show any clear change in comparison with the records taken during the pre-operative period.

After 6—16 days the ability to eat returned gradually and then the trained movements reappeared. In this period, at the beginning of a session the animals performed the trained movements and ate meat given as reinforcement, but, after a few minutes, they stopped eating, but still repeated many times the trained movement. This kind of hypophagia lasted for several weeks and in some cats for a few months, then, in most cases, the eating ability returned to its previous state.

The anatomical examination of the brains of this group of cats showed that the lesions were made in an area situated just in the front of and below the anterior commisure, over the optic chiasm, 1·5—2·5 mm to the side from the midline, involving part of the preoptic area (Fig. 2).

In other cats of this group only hypophagia developed and the trained movements were irregular and less frequent. In one cat a general disturbance of posture and movements was observed. The anatomical examination of the brains of these hypophagic cats showed that the lesions were assymetrical and involved other areas (Fig. 3).

Cats with lesions of the lateral hypothalamus. These animals were used as a control group in relation to the first. The behavior of these cats after operation was similar to that described previously (Anand and Brobeck 1951, Wyrwicka 1957, Morgane 1961, Teitelbaum and Epstein 1962, Balińska 1963). The animals did not eat in their home cages and had to be fed passively, as described above. This passive feeding was more difficult than in the rostral group, because of some defensive-aggressive attitude which developed usually in the lateral hypothalamic cats. However, their motor activity seemed to be generally lowered, the animals looked apathetic and remained motionless, sometimes in a strange "cataleptic" posture for a long time.

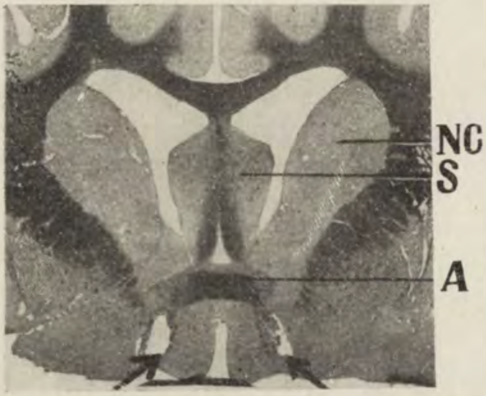

Fig. 2. Frontal section of the brain of cat No. 102, showing a typical bilateral lesion in the rostral hypothalamus, which resulted in aphagia with manifestations of the trained movements. Sites of lesions are indicated by arrows

A, anterior comissure, NC nucleus caudatus, S, septum

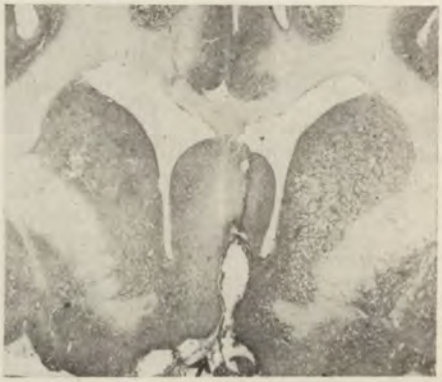

Fig. 3. Frontal section of the brain of cat No. 121, showing an atypical and assymetrical lesion resulting in hypophagia. The site of lesion is indicated by an arrow

Taken to the experimental cage, the cats did not perform their trained movements or eat. Neither did they pay any attention to the feeder or sniff or lick the meat, as cats of the first group sometimes did. The EEG records taken of two cats during the first week after coagulation showed a preponderance of α-activity and patterns similar to those appearing during drowsiness and sleep (Hess et al. 1953, Sterman et al. 1965). Whereas before operation desynchronizing patterns in the EEG record prevailed.

After several days of complete aphagia, the ability to eat actively gradually recovered, but hypophagia was present for several weeks or even months, until the animal was sacrificed. The trained movements reappeared usually some days after the recovery of active eating. In the beginning, partial, "abortive" movements, e.g. placing the foreleg on the food-tray instead on the platform which was located higher, were frequently observed. Such movements were not followed by food. Gradually, the instrumental reactions became correct, howevér for a long time they were less frequent and slower than before operation.

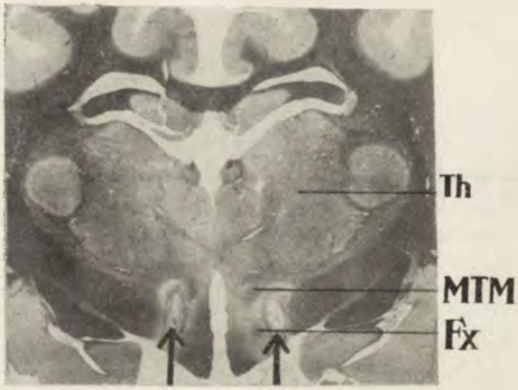

Fig. 4. Frontal section of the brain of cat No. 709, showing a typical lesion in the lateral hypothalamus, which resulted in aphagia and disappearance of the trained movements

F, fornix, TMT, tractus mammillo-thalamicus, Th, thalamus. The lesions are indicated by arrows

The anatomical examination of the brains of this group of cats showed that the lesions were made inside the area of the lateral hypothalamus and somewhat above, just laterally to the col. fornicis desc. and tractus mammillo-thalamicus (Fig. 4).

DISCUSSION

The main result of this paper is the presence of the alimentary instrumental reactions in aphagic cats after lesions of the rostral hypothalamus and the absence of these movements in aphagic animals after lesions of the lateral hypothalamus. A comparison of the results obtained in each group of animals suggests that lesions of the lateral hypothalamus destroyed some neural connections between the hypothalamic centers of feeding and the motor system, which may exist in this area. However, this is not the case in the rostral hypothalamus. This supposition is supported by the observation that the trained movements remain unchanged after rostral lesions, while these movements, reappearing after lateral hypothalamic lesions, are strongly injured and changed.

This hypothesis, however, does not explain why these movements appear in aphagic animals which refuse to eat. In normal animals the performance of the trained movements is a manifestation of the animal's desire to eat, and usually they do not appear when the animal is satiated. Therefore, it may be assumed that the rostral animals wanted to eat but could not take food because of some motor inablities or sensory disturbances. However, in most cases, the cats did not try to take food and, most frequently, after the performance of the trained movement, they did not even look at the food. For this reason, this supposition does not seem adequate.

Another explanation may be as follow. It was found that there exists in the vicinity of the area where the rostral lesions were made, a zone electrical stimulation of which elicits drowsiness and sleep in waking animals (Hess 1957, Sterman and Clemente 1962). The lesions in that area resulted in an increase of activity (Nauta 1946, Maire and Patton 1954, Sterman et al. 1964). It is possible that this area could have been injured with the rostral lesions and this was the cause of the general increase of the motor activity, observed in our rostral animals. This higher level of motor activity could facilitate the trained reaction which, in such case, could be evoked directly through the intercentral connections between the structures corresponding to the conditioned stimuli and the instrumental reaction, with the feeding center inactive (cf. Wyrwicka 1952, 1960, Dobrzecka and Wyrwicka 1960, Konorski and Dobrzecka 1962). Contrarily a low level of motor activity in the lateral-hypothalamic cats could suppress the possibility of the appearance of the trained movement.

SUMMARY

An instrumental reaction of placing the foreleg on a platform, reinforced by food, was established in 18 cats. Then, an area in the rostral part of the hypothalamus in 13 cats, and in the lateral hypothalamus in 5 cats, was destroyed by means of electrocoagulation. In most cats aphagia developed after operation. In aphagic lateral-hypothalamic cats the trained instrumental reaction disappeared completely, while the cats with rostral lesions performed the trained movement despite their refusal to take food. An explanation of these results is proposed.

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THE GENERALITY OF THE INCENTIVE-MOTIVATIONAL EFFECTS OF CLASSICALLY CONDITIONED STIMULI IN INSTRUMENTAL LEARNING *

W. E. BACON and D. BINDRA

National Institute of Mental Health, Bethseda, Maryland, U.S.A.,
McGill University, Montreal, Canada

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Much of the recent research on the relation between classical conditioning and instrumental behavior has been directed at finding out whether the occurrence of instrumental responses is necessarily dependent upon the simultaneous or prior occurrence of certain classically conditioned reactions. It now seems reasonably clear that the answer to this question is "No" (Black 1965, Miller and DeBold 1965, Williams 1965, Ellison and Konorski 1966, Bindra in preparation). Though classically conditioned reactions do not play a necessary role, other research has established that certain classically conditioned stimuli may have marked facilitative or inhibitory effects on the performance of instrumental responses (Walker 1942, Estes 1943, 1948), Herrenstein and Morse 1957, Morse and Skinner 1958, Marx and Murphy 1961, Bower and Grusec 1964, Zieliński and Sołtysik 1964, Trapold 1966). But little is known about the nature of such motivational effects of conditioned stimuli.

A conditioned stimulus (CS) that has been paired with a reinforcer (US) in a classical conditioning procedure can be shown to affect instrumental behavior in two ways. First, when that CS is presented as

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a reward at the end of an instrumental response, it facilitates the acquisition and performance of that response (Bersh 1951, Bugelski 1938, Saltzman 1949) and is described as a secondary reinforcing stimulus. Second, when the CS is presented prior to the initiation of an instrumental response, the CS may motivate the occurrence of the response (Dinsmoor 1950) and may be described as an instigational or incentive-motivational stimulus.

The purpose of the present investigation was to determine the effects of an incentive-motivational stimulus (i.e., a reinforcement-linked classical CS presented prior to response initiation) on the acquisition of an instrumental response, and to ascertain whether the effects would persist when the instrumental training was based on a drive different from that employed during classical conditioning. Earlier studies have dealt primarilly with CS effects during the course of extinction of the instrumental response under the same drive-reinforcement conditions.

EXPERIMENT I

The first experiment was designed to determine the effects of an incentive-motivational CS on the acquisition of an alley-running response, when both classical conditioning and instrumental training involved the same drive and reinforcement, that is, thirst-water. Control groups were included to assess any nonassociative effects of the CS and US presentations (Harris 1943).

Subjects. The subjects (Ss) were 40 male hooded rats, 73—83 days old at the start of the experiment. They were obtained from the Quebec Breeding Farm, St. Eustache, Quebec, and were housed in colony cages, 5—6 animals per cage.

Apparatus. Four identical experimental chambers were used for the classical conditioning aspect of the training procedure. Each chamber measured about 24 cm in length, 30 cm in width, and 20 cm in height and was housed in a sound-insulated metal chest. Water was delivered to a recessed receptacle in the side wall of the chamber by a liquid pump located outside the metal chest. The chamber was illuminated by a 10 watt house light and the CS (1000 cycle/sec tone) was presented through a 10 cm loudspeaker located in the side wall near the water receptacle.

Instrumental learning was carried out in a black enclosed right-turn L-shaped alleyway. The long arm of the alleyway was about 162 cm long, 25 cm high and 10 cm wide with the exception of the first 23 cm unit, which was 15 cm wide and served as the start box. The short arm was 36 cm long, 15 cm wide, and 25 cm high and served as the goal box. Starting time, the interval between the opening of the start-box door and the interruption of a photo-electric beam located 6 cm beyond the door, and running time, the interval between the interruption of this beam and a second similar beam 105 cm further down the alley, were measured to the nearest ·01 sec. The side wall of the start box contained a 2·5-cm diameter hole covered with perforated tape, which hid a 10 cm loudspeaker located behind the hole. A drinking tube projected from a hole in the far wall of the goal box.

The auditory stimuli were presented through the loudspeakers at a sound pressure level of 80±2 db re .0002 dyne/cm². Appropriate programming and timing equipment determined the presentation and duration of auditory stimuli and the presentation of water in the chambers, and similar timing equipment controlled the duration of the stimuli in the alleyway.

Procedure. Upon receipt from the breeder, Ss were placed on normal food and water diet and gentled. Three days later, a 22—23 hr. water deprivation schedule consisting of 1/2 hr access to water daily was initiated and continued throughout the experiment.

The Ss were allowed 12 days to adapt to the water-deprivation schedule before the start of classical conditioning. During this conditioning each S was given daily 30-min. sessions for 12 days under one of four treatments. The experimental treatment (E) consisted of a standard classical conditioning procedure where the offset of 15-sec 1000 cycle/sec tone (CS) was immediately followed by approximately 1/3 cc of water (US); this CS-US pairing was presented on a variable-interval schedule with the reinforcement available on the average every 2 min. (VI 2 min. schedule). The remaining three treatments were control procedures. In the noncontingent or random-order treatment (N), the CS was presented in the same manner as described above but the US was programmed on a different VI 2 min. schedule such that CS and US were never paired. In the water only treatment (W), Ss were not exposed to the CS but were given the US on a VI 2 min. schedule. In the tone only treatment (T), Ss were presented with the CS on a VI 2 min. schedule but the US was not presented.

Instrumental learning trials in the alleyway followed the 12 sessions of classical conditioning. On the first day, Ss were placed in pairs in the goal box for 2—3 min. access to water. On the second day, Ss were placed in the goal box singly for 1—2 min. access to water. Training proper began on the third day and continued for 8 days. All Ss were given 5 trials per day with a 15—30 sec intertrial interval and 20—30 sec. access to water in the goal box. On each trial S was confined for 15 sec in the start box before the door was opened. During this confinement, all Ss received the CS, a 15-sec 1000-cycle/sec tone, with the exception of half the E treatment Ss. Thus there was a total of 5 groups of 8 Ss each designated according to their treatment as E, N, W, T, and C. The letter C refers to the group that received the E treatment during classical conditioning but was not exposed to the CS during instrumental learning.

Results. Both starting and running times in the alleyway were separately averaged in blocks of 10 trials for each animal and analyses of variance carried out. A Lindquist Type I analysis of the starting time data indicated a significant Group effect ($F = 3{\cdot}03$, $df = 4/35$, $p < .05$), Trial Block effect ($F = 9{\cdot}90$, $df = 3/105$, $p < .01$), and Group × Trial Block interaction ($F = 6{\cdot}22$, $df = 12/105$, $p < .01$). The Trial Block effect ($F = 22{\cdot}48$, $df = 3/105$, $p < .01$) and the interaction ($F = 4{\cdot}58$, $df = 12/105$, $p < .01$) also proved significant in the running time analysis.

Figure 1 graphically depicts the Group × Trial Block interactions. The starting and running times decreased across trials to approximately the same terminal level for all groups but the performance levels of the different groups on the early trials (particularly Trial Block 2) were not the same. Close examination of the Figure reveals that the performance curves fall into two distinct groupings. The starting and running times of Groups E, C, and W were almost identical on each Trial Block and were, at least initially, lower than the corresponding times of Groups N and T. Approximate t-tests (Lindquist 1953) indicated no statistically significant differences ($p > .05$) between Groups E, C, and W or between Groups N and T on any Trial Block. On Trial Block 2, all Groups E, C, and W vs. Groups N and T comparisons were significant (p's $< .05$) with the exception of the Group T. vs. Groups E and W comparisons for the running time measure. In addition, Groups N and T showed little or no improvement in mean response times from Trial Block 1 to Trial Block 2 particularly in reference to the starting time

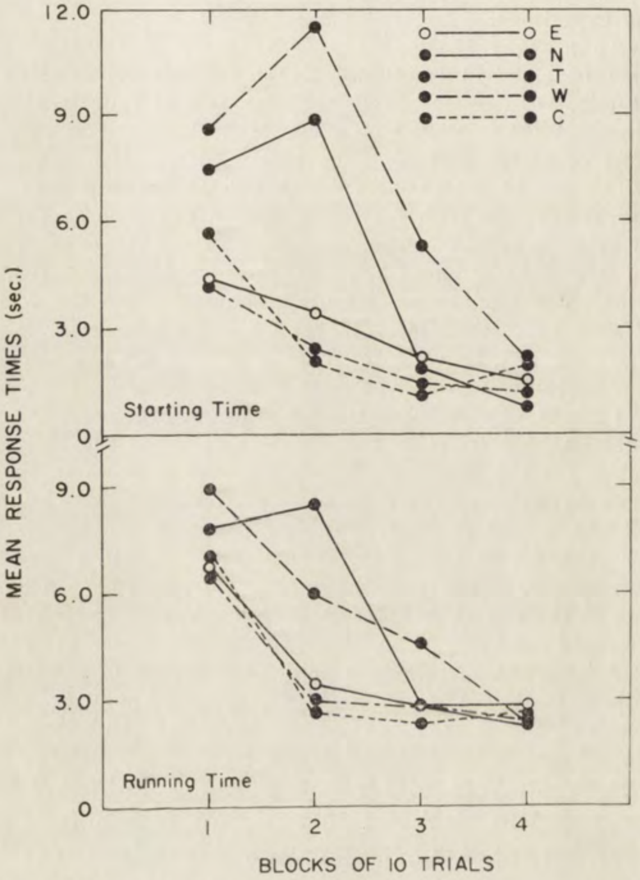

Fig. 1. Mean starting and running times during acquisition trials for the Experimental (E), Noncontingent (N), Tone Only (T), Water Only (W), and Control (C) groups

measure. Only 10 out of 16 Ss in the combined N and T group were faster in starting on Trial Block 2 than on Trial Block 1 (Sign Test, $p > .50$) whereas 22 out of 24 Ss in the combined E, W, and C group were faster (Sign Test, $p < .001$).

EXPERIMENT II

The purpose of this experiment was to determine whether the incentive-motivational properties of a CS, generated by pairing it with water in thirsty rats, would affect the acquisition of an instrumental response on the basis of another drive-reinforcement combination, hunger-food.

Subjects and apparatus. The Ss were 28 naive male hooded rats, 73—83 days old at the start of the experiment. The apparatus was the same as that used in Experiment I.

Procedure. The handling routine, as well as the deprivation schedule through the classical conditioning phase of the experiment, was identical to that used in Experiment I. The classical conditioning procedure was similar to that of Experiment I with the exception that daily 45 min. (rather than 30-min.) sessions were given with VI 3 min. (rather than VI 2 min.) schedules of CS and US presentation. Half the Ss received the E (CS-US pairing) treatment, and the remaining Ss, the N (noncontingent) treatment.

Immediately following the last day of classical conditioning, 8 E and 8 N Ss were switched from the water deprivation schedule to a food deprivation schedule consisting of continuous access to water and $^1/_2$-hr. access to food daily. The remaining 6 E and 6 N Ss were continued on the water deprivation schedule.

Instrumental training in the alleyway began 5 days later. The thirsty Ss were trained with the CS presentation in the start box exactly as the SS in Experiment I. The hungry Ss were trained in a similar manner with the exception that on each trial two .045 gm Noyes food pellets were given as reward in the goal box.

Thus, there were four experimental groups in a 2×2 factorial design: N-S, N-C, E-S, and E-C. The first set of letters represents the classical conditioning treatment and the second set indicates whether the drive-reinforcer system remained the same from the classical conditioning to the instrumental training phase (S) or whether the system was changed (C).

Results. Starting and running time means for blocks of 10 trials were computed for each S. First, Lindquist Type III analyses were carried out comparing the data from the E and N Ss of Experiment I with the E-S and N-S Ss of the present experiment to determine whether the slight changes made in the classical conditioning procedure had any effect on alleyway performance. Neither the main effect of the Experiment variable nor any of its interactions with the Treatment or Trial Block variables proved statistically reliable ($p\text{'s} > .10$) for either time measure.

As there were no detectable performance differences due to these procedural variations between experiments, the data from the E and N conditions of Experiment I were combined with those from the E-S and N-S conditions, respectively. The resulting pooled data and the Group E-C and N-C data were then analyzed by means of Lindquist Type III analyses to determine the main and interactive effects of the Treatment (E vs. N), Drive (S vs. C), and Trial Block variables. The Treatment × Trial Block interactions were significant for both measures (start time: $F = 3{\cdot}05$, $df = 3/120$, $p < .05$; running time: $F = 3{\cdot}06$, $df = 3/120$, $p < .05$), as were the Trial Block main effects (start time: $F = 18{\cdot}41$, $df = 3/120$, $p < .01$; running time: $F = 22{\cdot}00$, $df = 3/120$,

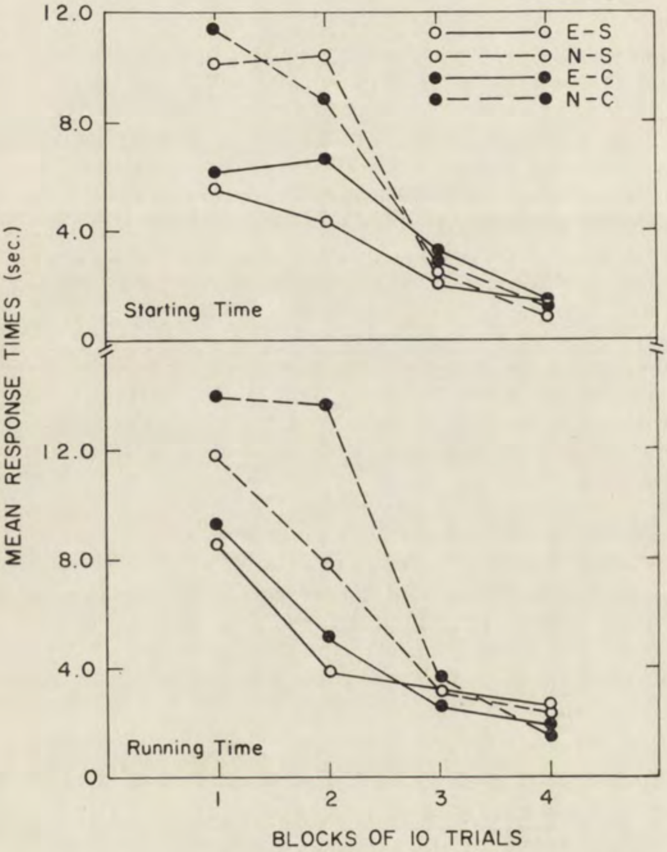

Fig. 2. Mean starting and running times during acquisition trials for the Experimental-Same (E-S), Experimental-Change (E-C), Noncontingent-Same (N-S), and Noncontingent-Change (N-C) groups. The first word describes the classical conditioning contingency, and the second indicates whether the drive remained the same or was changed from the classical conditioning to the instrumental training situation

$p < .01$). The Treatment main effect approached significance (start time: $F = 3{\cdot}24$, $df = 1/40$, $p < .10$; running time: $F = 2{\cdot}84$, $df = 1/40$, $p < .10$). In no case did the Drive variable or its interaction with the Treatment and Trial Block variables approach conventional levels of significance. Figure 2 summarizes these results. On the initial alleyway trials the N Ss performed the instrumental response at a slower speed than E Ss regardless of whether the deprivation-reinforcer conditions remained the same from classical conditioning to instrumental training or were changed from thirst and water to hunger and food.

Thus, it may be concluded that a CS that has acquired incentive-motivational properties in connection with a thirst-water drive-reinforcement combination can affect the learning of an instrumental response on the basis of a hunger-food drive-reinforcement combination. Change in the type of drive does not alter the effectiveness of an incentive-motivational CS.

EXPERIMENT III

This experiment was designed to determine whether the incentive-motivational properties of a CS, acquired in connection with a positive reinforcer (water), would affect the acquisition of an instrumental response involving aversive stimulation. The instrumental response was running to avoid an electric shock.

Subjects and apparatus. The Ss were 20 naive male hooded rats, 73—83 days old. The classical conditioning apparatus was the same as was used in the previous experiments.

A wooden L-shaped alleyway was used for avoidance training. The alleyway was 15 cm wide and 10 cm high and consisted of a stem about 44 cm long and a right-turn arm 50 cm long. The first 17 cm unit of the stem served as a start box and was separated from the remaining stem by a Plexiglas guillotine door. The last 27 cm unit of the arm functioned as a goal box and was separated from the remaining arm by a top-hinged swinging door. The floor of the alleyway was a grid composed of rods of 0·4-cm diameter set 1·5 cm apart; in the goal box a wooden platform covered the grid. The grid could be electrified by means of a shock generator-scrambler. Auditory stimuli could be presented by means of a 10 cm loudspeaker located just behind the start box. The opening of the guillotine door started a running time meter which stopped when S interrupted a photoelectric light beam situated 15 cm past the door. The meter provided a measure of starting latency.

Procedure. Two groups of 10 Ss received a treatment identical to the Group E and Group N Ss in Experiment I through the classical conditioning phase of the experiment.

Avoidance training in the maze commenced on the day following the last classical conditioning session. Each S received 10 trials per day for 5 days with approximately a 30-sec intertrial interval. On each trial, S was confined in the start box for 15 sec during which time the CS was presented. The start box door was raised at the termination of the CS. If S failed to leave the start box within 3 sec, a 0·8 ma shock was delivered through the grid, until S entered the goal box. If S interrupted the light beam within the 3 sec interval no shock was delivered and the trial was considered to be a successful avoidance trial. The Ss were removed from the goal box 5—10 sec after entry.

Results. A criterion of 10 successful avoidances out of 10 trials on a given day was selected prior to the experiment as indicative of avoidance learning. As only 12 Ss achieved this criterion, 8 of which had received the E treatment, a somewhat less stringent criterion of 9 out of 10 was then adopted. Three Ss of the N group failed to meet this criterion and were assigned an arbitrary score of 6 days for statistical analysis. Table 1 shows the median day on which the criterion was reached for each group; the difference between groups was statistically significant ($U = 14{\cdot}5$, $p < .02$). The N group required twice as many days as the E group to reach the shock avoidance criterion.

Table

Median Number of Days to Avoidance Criterion and Mean Starting Latency for the Experimental and Noncontingent Groups

	Median Day to Avoidance Criterion	Mean Starting Latency
Experimental Group	2	2.1
Noncontingent Group	4	2.7

The starting latencies for each S on each day were averaged and these means were subjected to an analysis of variance. This analysis indicated that (1) starting latencies improved across days ($F = 30.51$, $df = 4/72$, $p < .01$); (2) the difference in performance between the E and N Ss did not quite reach a conventional significance level ($F = 3.37$, $df = 1/18$, $p < .10$); and (3) this performance difference between the two groups did not change appreciably across days ($F = 1.09$, $df = 4/72$, $p > .10$). Table presents the mean starting latencies averaged across the 50 avoidance trials. Although not great, there is some suggestion that Group N Ss left the start box more slowly than Group E Ss throughout avoidance training. These data are consistent with the hypothesis that the incentive-motivational CS affected the acquisition of the avoidance response.

DISCUSSION

If one compares only the groups conventionally employed as "controls" (Groups N and T) with the experimental group (Group E) in Experiment I, then it would seem that the positive incentive-motivational

CS facilitated the acquisition of the alley-running instrumental response. However, in light of the Groups W and C, which learned as quickly as Group E, it is clear that the difference in speed of learning is not attributable to an incentive-motivational effect of CS per se.

One possibility is that the groups that received the US (water) in the classical conditioning situation (E, N, W, and C) were conditioned to the whole complex of situational cues connected with the daily experimental procedure. Thus the positive incentive-motivational properties of situational cues may have been sufficient to facilitate the acquisition of the instrumental response in the case of Groups W and C. Since Group T Ss received no US during the classical conditioning sessions, no facilitatory effects could be expected and none were found. The poor performance of Group N then requires another explanation. It may be that, in this case, the CS became a signal for no US, as the CS and US were never paired (negative conditioning), and thus produced an inhibitory effect which cancelled the facilitatory effect of the positive incentive-motivational situational cues. The existence of negative conditioning has been mentioned in other recent studies (Cornell and Strub 1965, Jenkins 1965).

In contrast to the interpretation in terms of a positive incentive--motivational factor, one could speculate that the results reflect the operation of only a negative (inhibitory) incentive-motivational factor. Groups N and T were the only groups exposed to the CS during both classical conditioning and instrumental training in which the CS was never closely followed by the US during classical conditioning. There is ample evidence (see Thorpe 1963) that repeated presentation of a stimulus (CS) which is not followed by any kind of reinforcement (US) results in habituation, that is, a decline in responsiveness to that stimulus. There is also some evidence (Konorski and Szwejkowska 1950, 1952; Lubow and Moore 1959, Lubow 1965, Szwejkowska and Konorski 1959) that nonreinforced pre--exposure to a to-be-conditioned stimulus results in an acquisition decrement during the subsequent conditioning of a response to that stimulus. This evidence in conjunction with our findings that Groups N and T showed little or no improvement in the early instrumental training trials suggests that an inhibitory factor may have produced the differences between the groups. The pairing of the CS and US (Group E), or nonexposure to the CS during classical conditioning (Group W) or instrumental training (Group C) would protect the remaining three groups from an inhibitory effect.

Regardless of whether the differences between Groups E and N are due to positive incentive-motivational effects (facilitation) or negative incentive-motivational effects (inhibition), or a combination of both, the results of Experiments II and III indicate that these differences were not directly related to the similarity of drive-reinforcer conditions between the classical conditioning and instrumental learning situations. Whatever the nature of the motivational factor that affects the acquisition of the instrumental response, the factor clearly generalizes from thirst—water to hunger—food and shock—escape. This finding would seem to argue against theories that postulate mediating responses or intervening variables defined in terms of specific drives or specific consummatory responses. Even the demonstration (Verplanck and Hayes 1953) that water-deprivation operations lead to some restriction of food intake, or the assumption that similar interoceptive stimuli result from water and food reinforcers, would not aid such theories in explaining the persistence of the incentive-motivational effect when the change is made from an appetitive to an aversive drive (Experiment III).

A question raised by the present findings concerns the drive conditions necessary for realizing incentive-motivational effects. Estes (1948, 1949) early work on the conditions necessary for obtaining secondary reinforcing effects led him to suggest that a change in drive state would not prevent the generation of such effects so long as any strong drive was present. The fact that in Experiment II the incentive-motivational effects persisted with a change in drive from thirst to hunger is consistent with this suggestion. And since in Experiment III avoidance training was given while the animals were thirsty, the drive may have contributed to the generation of the observed incentive-motivational effects. However, the present results do not answer the question whether the drive affects instrumental behavior by increasing the incentive-motivational effect or whether it acts independently of incentive-motivation. The question of the combination or interaction of drive and incentive-motivational effects requires further exploration.

Bindra and Palfai (1967) suggest that positive and negative incentive-motivational CS's affect instrumental behavior by producing positive and negative central motivational states, which promote action and inaction, respectively. These motivational states may be regarded as general excitatory and inhibitory tendencies created centrally, such as those postulated by several investigators (see Gerbrandt 1965, for review). This view implies that whenever a positive or negative state is created facilitation or inhibition effects may occur in the performance of instrumental responses. The exact nature and extent of the effect would naturally depend upon such factors as whether the response is an active response or has some inactive components (e.g., delayed response) and response topography (Bindra 1961). It also follows from this view that the incentive-motivational effects would occur whether or not the drive-reinforcement conditions for instrumental training are the same as those prevailing during classical conditioning.

SUMMARY

We studied the effects of a CS (a tone), previously paired (classical conditioning procedure) with a reinforcer (water), on the acquisition of an instrumental running response in the rat. In Experiment I (40 rats) the instrumental response was trained on the same drive-reinforcement combination (thirst-water) as was used during classical conditioning; in Experiment II (28 rats) the drive-reinforcement combination was changed to hunger-food during instrumental training; and in Experiment III (20 rats) to electric shock-escape. In all cases the prior pairing of CS with water resulted in more rapid acquisition of the instrumental response in comparison to the procedure of not pairing the CS with water. Both incentive-motivational facilitation and incentive-motivational inhibition can account for the results. Both these interpretations are consonant with the view that incentive-motivational (reinforcement-linked) stimuli create general central exitatory and inhibitory states which directly influence behavior.

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DIFFERENTIATION BETWEEN SAME TONE COMPOUND VERSUS LOW-HIGH TONE COMPOUND IN DOGS

Hanna CHORĄŻYNA

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

(Received November 28, 1966)

For the investigation of recent memory of stimuli Konorski (1959, 1961) has proposed a test in which various pairs of successive stimuli are differentiated in a conditioning procedure. If two differentiated compound CSs differ in the relations between their components and not in their absolute values, then obviously the subject has to remember the first component in order to react correctly to the second one.

In our experiments on the recent memory of auditory stimuli this test was applied in the following form (Chorążyna 1959). Two tones were presented to the dogs in successive order with an interval of a few seconds. The frequency of tones presented was different in different trials; however, if the two components of the pair were identical, the compound CS was followed by food, whereas when they were different the compound CS was not reinforced. A simple instrumental act of placing the right foreleg on the feeder was the indicator of the animal's responding. This sort of differentiation turned out to be very difficult for the dogs and they only solved the problem after a training of many hundreds trials.

Further experimentation along this line (Chorążyna and Konorski 1962) suggested that the great difficulty of the aforementioned differentiation was not inherent in the test itself, i.e. in the deficiency of the dog's recent memory, but was rather due to certain unessential properties of the task applied. To clear up this possibility, in the present work a comparison of the course of differentiation was made in two experimental procedures. In one procedure the compound of two identical tones was the positive CS and the compound of lower-higher tones was the negative CS. In the second one the lower-higher tone compound was positive and the same tone compound was negative. It turned out that this apparently small procedural difference played a decisive role in the difficulty of differentiation.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were performed on 14 dogs in a regular sound-proof CR chamber. CSs were tones of varying frequencies but same intensity (about 70 db) emitted from an acoustic generator. The tones were presented always in successive pairs. Each component of the pair lasted 2 sec and they were separated by 3 sec intervals. The instrumental food CR procedure was used, the trained movement being the lifting of the right foreleg and placing it on the feeder.

The dogs were divided into two groups. Group I, consisting of ten animals, was trained in the differentiation task in which the compound of two identical tones (henceforth called S_x—S_x) was positive and the compound of lower-higher tones (henceforth called S_x—S_y) was negative. Group II, consisting of four dogs, was trained in the reverse task, i.e. the lower-higher tone compound (S_x—S_y) was positive whereas the same tone compound (S_x—S_x) was negative.

At the beginning of training only positive compounds were presented. In group I the CS originally trained was the compound 200 cycle/sec — 200 cycle/sec, whereas in group II it was the compound 200 cycle/sec — 1800 cycle/sec. Nine trials per session were given with intertrial intervals of 1—2,5 min.

The original training consisted in teaching the animals, by the method of passive movements, to lift the right foreleg and place it on the feeder situated in front of the animal to the second component of the compound CS. After the movement was performed, the bowl with food (pieces of bread soaked in broth) was put into position by an automatic device.

After several such sessions the dogs started to perform actively the trained movement to both components of the compound CS as well as in the intertrial intervals. In order to discourage the animals from performing the movement to the first component of the compound, we occasionally, when the dog did so, discontinued the first tone and the second was not presented.

When the animals learned to place the foreleg on the feeder to the positive CS, the negative compound CS was introduced. It was 200 cycle/sec — 1800 cycle/sec in group I and 200 cycle/sec — 200 cycle/sec in group II. The negative trials were introduced gradually, at the beginning only once daily, and then, if the dog remained calm, they were increased to two to five times daily, interspersed by the positive trials. If the differentiation training caused restlessness and preneurotic symptoms (which occasionally occurred in dogs of group I), the number of negative trials per day was limited and the dog obtained small doses of bromides half an hour before a session. Those dogs (belonging only to group I) which developed strong and incurable experimental neurosis were discarded.

When the positive conditioned responses occurred only to the second component of the positive compound CS, and the negative responses (i.e. no movement) to the negative compound CS were correct in at least 70% of trials, the frequency of tones in the S_x—S_x compounds was gradually increased up to 2000 cycle/sec. Of course these compounds were also positive in group I and negative in group II. When to the second component of the positive compound the animal did not perform the trained movement, this compound was nevertheless reinforced "gratis" by food. This was done because, according to Wyrwicka's findings (1952), this procedure leads to the transfer of the instrumental response to the reinforced stimulus.

In the last stage of training the frequencies of the S_x—S_y tone compounds were also changed in that the difference between the two tones was diminished as much as it was possible for the given animal. Eventually, the stage was reached in which in a given session each trial was different and the only cue determining the animal's response was the sameness of the tones or their difference.

RESULTS

From the very beginning of training a spectacular difference was manifested between the dogs of group I and group II. As shown in Table the dogs of group I required much more trials than the dogs of group II in order to inhibit the conditioned responses to the first component of the positive compound.

Table

The number of trials required to inhibit the conditioned response to the first component of the compound CS

Group I		Group II	
No. of dog	Number of trials till criterion*)	No. of dog	Number of trials till criterion*)
1	161	11	36
2	99	12	21
3	175	13	47
4	172	14	15
5	138		
6	125		
7	112		
8	97		
9	119		
10	173		
Mean	137	Mean	29,7

* By criterion three successive experimental sessions are taken in which the number of errors was less than 25%.

When the negative compound was introduced a clear difference between the performance of group I and group II was again manifested. As seen in Fig. 1 the animals of group I displayed to the negative compound a full and consistent positive response, whereas the animals of group II inhibited the instrumental response already in the first 10 trial block. When the frequencies of tones in the S_x—S_x compound were increased (which is denoted in Fig. 1 by arrows), the disinhibition of the already established inhibitory CR was again much stronger in group I than in group II. Finally, the ultimate result of training was also different in each group (Fig. 1 and 2). Whereas all the animals of group II reached 100% criterion of correct responses, no animal of group I achieved this level of performance. This means that even when a steady state of performance was achieved the dogs of group I again and again committed errors in negative trials and the correct inhibitory responses oscillated between 80% and 90%.

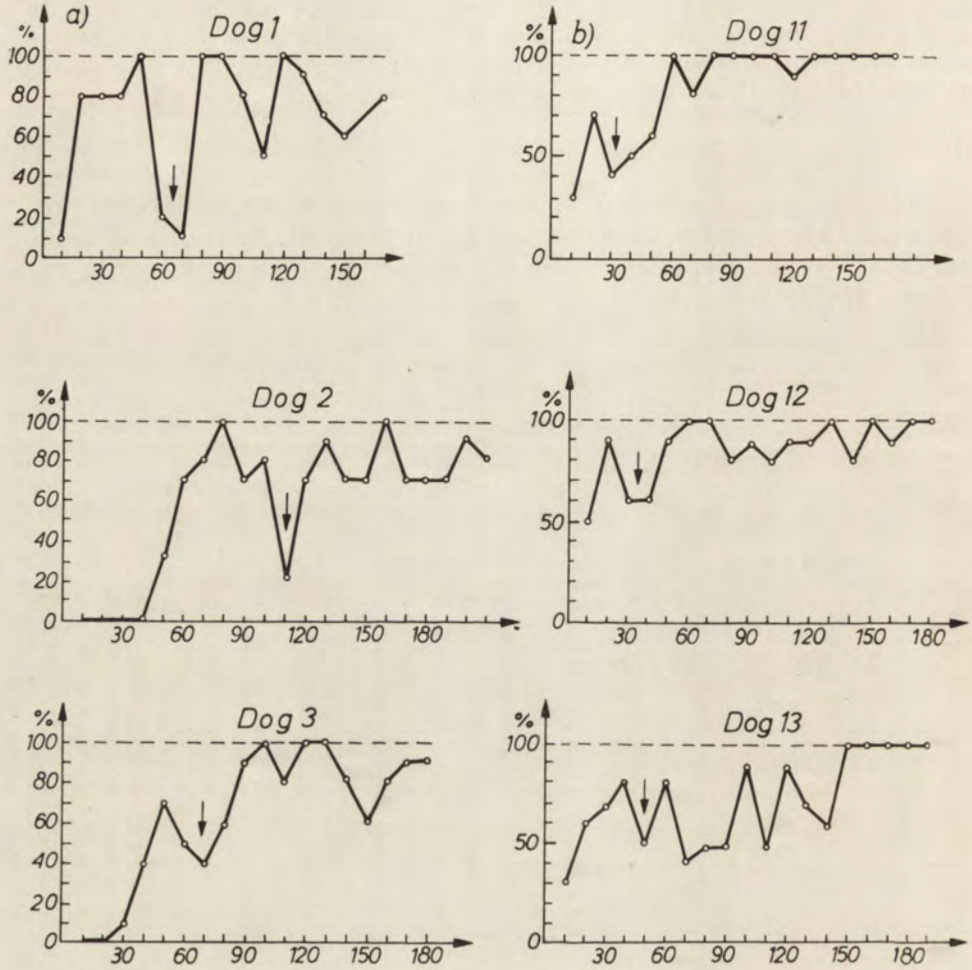

Fig. 1. The typical course of inhibitory training in three dogs of group I (a) and in three dogs of group II (b)

Abscissae, successive blocks of ten negative trials; ordinates, the percentage of correct (i. e. inhibitory) responses. The arrow on each graph denotes the presentation of tones of increased frequency in $S_x - S_x$ compound.

As far as the positive trials are concerned the performance of both groups was correct (except occasional disinhibition of the first component of the compound). This was due to the fact that in our experimental procedure the number of positive trials prevailed over the number of negative, this number being regulated in such a way as not to disturb the responses to the positive compound.

A general observation of the behavior of our experimental animals during sessions revealed a consistent and considerable difference between the individuals of group I and group II. The dogs of group I displayed a continuous restlessness during the whole training which was manifested in whining, stereotype "displacement" movements and occasional refusal to take food from the bowl. Seven of them received regularly small doses of bromides. When the number of negative trials did not exceed one or two per session, their behavior was tolerable, but any attempt to increase that number led to strong behavioral disturbances. On the other hand, the training of the dogs of group II occurred without, any conflicts. They were always quiet and an increase of negative trials to five or more per session was quite harmless to them.

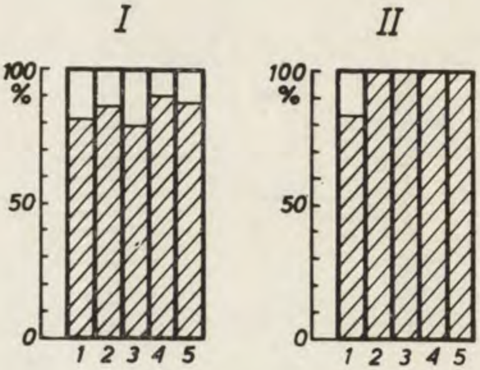

Fig. 2. The performance of the dogs of group I and II in 50 negative trials at the end of training

Each column denotes ten negative trials. The hatched parts of columns denote the average number of correct (inhibitory) responses in a given block. Note that all the animals of group II reacted correctly in the last 40 trials, whereas the dogs in group I continued to make errors in 10%—15% of trials.

The excellent performance of the dogs of group II allowed us to carry out special tests in which the intervals between the components of the compound CSs were prolonged. In all these dogs these intervals were easily protracted to 15 sec without any deficit of their performance. In one dog the limit of the intracompound interval was tested. It turned out that with a 30 sec interval the animal was still able to react correctly, but when this interval was regularly applied the animal's performance deteriorated and it was necessary to return to 10—15 sec intervals. Needless to say, in animals of group I even a very small increase of intervals beyond 3 sec was detrimental for their CR performance.

DISCUSSION

As was found in our preceding study (Chorążyna and Konorski 1962), when the dogs are confronted with a tone differentiation task which can be solved either on the basis of the absolute pitch of the tones or on their comparison, they always utilize the former cue and not the latter. Even when the task requires the utilization of the comparative cues, the animals stick to the absolute cues and this strategy makes the solution of the task more difficult.

This principle played an important role in the whole course of the present experiments and helped us to understand the striking difference between the differentiation task in our two groups of dogs (S_x—S_x positive, S_x—S_y negative in group I; and S_x—S_y positive, S_x—S_x negative in group II).

It has been shown that the difference between the difficulty of both tasks became manifested already in our original training in which the animals were taught to react only to the second component of the compound CS and to abstain from reacting to the first component. When the compound CS consisted of two identical tones (200 cycle/sec) the animals displayed a strong tendency to react already to the first component because of its identity with the second tone. This difficulty did not exist when the compound consisted of two different tones (200 cycle/ sec), because the animals could base their differential response on the absolute frequency of each tone.

When the negative compound CS was introduced into the training the animals of group I were again handicapped in comparison to those of group II. In fact, in group II the negative CS consisted simply in the repetition of the tone 200 cycle/sec which was made negative in the original training. On the contrary, in group I the negative CS consisted in substitution of the tone 200 cycle/sec by 1800 cycle/sec in the second component of the compound. In consequence this CS produced by generalization a positive response. Thus the dogs had to learn that the tone 1800 cycle/sec put in the second place of the compound is negative, whereas the tone 200 cycle/sec remains positive. The conflicting situation was here obvious in view of the fact that this tone was negative when presented first.

In the next stage we began to increase the frequency of S_x—S_x compound. This produced a disturbance of the already established negative CRs in both groups. In group I the reinforcement of high tones when presented in the S_x—S_x compound led to disinhibition of the second component in the negative S_x—S_y compound. In group II in which the S_x—S_x compound was negative, an increase of the frequency of S_x led to its disinhibition because the high tones were positive in the S_x—S_y compounds. In this stage the animals had to base the solution of the differentiation problem exclusively on the recent memory of the first component of the compound when the second component was presented, because the absolute values of the particular tones did not provide any cues for this solution.

Why was it that in this stage the S_x—S_x positive, S_x—S_y negative differentiation task continued to be so much more difficult and unstable than the reverse task? The answer to this question lies again in the sameness of the two tones in the positive compound in group I. When S_x is presented as the first component of the compound, it is strongly negative regardlesss of its absolute value because during the whole course of training the animals were taught that whatever the frequency of this component, it was never directly followed by food. Therefore, the repetition of that stimulus in the S_x—S_x compound ipso facto tended to produce a negative effect. On the other hand, presentation of a different stimulus S_y had a purely positive significance, since it was the second component and in addition it was different from the preceding negative stimulus. In consequence, the training conducted in group II followed obviously the natural relations between the stimuli, the second component of the positive compound producing arousal because of its "oddity" in respect to the first negative component. Contrarily the differentiation training conducted in group I had an inherent conflict, since the animal had to break the negative character of the S_x stimulus presented for the second time, and inhibit the more natural positive response to stimulus S_y.

In conclusion we see that the difficulty of the task presented in group I is not connected with the limited scope of recent memory in dogs but is due to the inappropriate programming of the experimental procedure. The long intracompound interval available in animals of group II shows that with a proper procedure a much better performance in the recent memory test may be achieved.

SUMMARY

1. In two groups of dogs the go-no go differentiation was trained to the successive compound stimuli S_x—S_x versus S_x—S_y in which S_x was a tone of any frequency and S_y was a tone higher than S_x. In group I the S_x—S_x compound was positive and the S_x—S_y compound negative, in group II the compound S_x—S_y was positive and S_x—S_x negative.

2. The S_x—S_x positive, S_x—S_y negative differentiation turned out to be very difficult, requiring a prolonged and very cautious training. It

frequently led to experimental neurosis and never became stable and reliable. On the contrary, the S_x—S_y positive, S_x—S_x negative differentiation was relatively easy and occurred without any complications. It never led to an experimental neurosis and once established displayed 100% correct responses. The negative trials could be given many times without any harm to the animal's performance and the intervals between the components of the compound could be prolonged to 15 sec or more.

3.The reasons for this spectacular difference between the two kinds of differentiation are discussed.

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RESEARCH ON NEUROPHYSIOLOGY IN POLAND IN THE YEARS 1964—1966

B. ŻERNICKI[1]

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

(Received October 25, 1966)

In the present review, the term "neurophysiological research" is used in the broad sense, covering essentially neurophysiology sensu stricto, neurofarmacology and behavioral investigations. In addition, some neuroanatomical studies, related to the neurophysiological investigations, are included. The investigations carried out by Polish neurophysiologists abroad are also mentioned. The references to the addresses of the investigators are given in brackets.

I. BEHAVIOR

1. Orientation reflexes (Dreher et al. 1965, 1966, Stępień and Stępień 1965, Żernicki and Dreher 1965, Zieliński 1966a, Konorski 1967, Żernicki et al. 1967) [1].

2. The low of stimulus strength (Zieliński 1965ab, 1966a) [1].

3. Classical conditioned reflexes (Baldwin and Sołtysik 1966, Wolf 1966, Konorski 1967) [1, 10].

4. Instrumental conditioned reflexes (Konorski 1964, 1967, Krause et al. 1964, Zieliński and Sołtysik 1964, Romaniuk 1966, Wyrwicka 1966, see also references 1, 2 and 3 in the next Section) [1, 10, 16, 24].

5. The relations between classical and instrumental conditioned reflexes (Ellison and Konorski 1965, 1966, Sołtysik and Konorski 1966, Konorski 1967) [1].

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[1] Secretary, Neurophysiological Board, Committee of Physiological Sciences, Polish Academy of Sciences, Warsaw 22, Pasteura 3.

6. Internal inhibition (Brutkowski and Dąbrowska 1965, Kozak 1965, Zieliński 1966c, Konorski 1967, see also references 1 and 3 in the next Section) [1, 10, 24].

7. Cues in various forms of differentiation (Ławicka 1964, Dobrzecka et al. 1966) [1].

8. Alternation conditioned reflexes (Szwejkowska et al. 1964, Szwejkowska 1965ab) [1].

9. Return reaction (Łukaszewska 1964ab, 1966ab) [1].

10. Fatigue of conditioned reflexes (Cytawa 1964, 1965, 1966, 1967, Sadowski 1964) [3, 11].

11. EEG activity in conditioning (Buchwald et al. 1964, Clemente et al. 1964, Jus and Jus 1964) [1, 15].

12. Behavioral and EEG effects of psychotropic drugs (Kleinrok 1964, Wojtczak-Jaroszowa 1964, Gryglewski et al. 1965, Kostowski et al. 1965, Sierosławska 1965) [8, 13, 17, 22].

II. BRAIN FUNCTIONS

1. Prefrontal cortex (Dąbrowska 1964, Brutkowski 1964, 1965, 1966abc, 1967, Konorski and Ławicka 1964, Wolf 1964, 1966, Dziurdzik 1965, Szwejkowska 1965b, Szwejkowska et al. 1965, Balińska 1966ab, Balińska et al. 1966, Brutkowski and Dąbrowska 1966ab, Cieśliński et al. 1966, Jaworska and Sołtysik 1966, Ławicka et al. 1966, Łukaszewska 1966b, Zieliński 1966b, Narkiewicz and Brutkowski 1967) [1, 10, 20, 24].

2. Motor system:
   a) Frontal oculo-motor cortex (Dreher et al. 1965, Dreher and Żernicki 1967) [1].
   b) Sensori-motor cortex (Kreiner 1964, Dobrzecka et al. 1965, Jankowska and Tarnecki 1965, Stępień and Stępień 1965, Stępień et al. 1966) [1, 12].
   c) Pyramidal tracts (Górska et al. 1966ab, Górska 1967) [1].

3. Limbic system:
   a) Amygdala (Fonberg 1965, 1966ac, 1967a, Miodoński 1965, Brutkowski 1966a) [1, 12].
   b) Septum (Liss and Łukaszewska 1967, Miodoński 1967) [1, 12].
   c) Hypothalamus (Balińska et al. 1964, 1966, Lewińska 1964, 1967, Marczyński et al. 1964, Wyrwicka 1964, Balińska 1965, 1966a, Romaniuk 1965ab, Teitelbaum and Cytawa 1965, 1967, Wyrwicka and Do-

brzecka 1965, 1966, Brutkowski 1966c, Domański et al. 1966, Fonberg 1966b, 1967b, Lewińska and Romaniuk 1966, Śmiałowski 1966, Traczyk and Jakubowska 1966, Wyrwicka and Doty 1966, Balińska and Brutkowski 1967, Domański and Kochman 1967, Traczyk 1967) [1, 3, 8, 10, 11, 18].

4. Visual system (Dreher et al. 1965, Kozak et al. 1965, 1967, Campbell and Kulikowski 1966, Campbell et al. 1966, Gawroński 1966, Gawroński and Konorski 1966, Konorski 1967) [1, 5].

5. Caudate nucleus (Buchwald et al. 1964, Horvath et al. 1964, Traczyk and Sadowski 1964) [1, 3, 18].

6. Ascending reticular system (Sadowski 1965, Santibanez and Żernicki 1967, Sobieszek 1966ab, Żernicki et al. 1967) [1, 3].

7. Isolated cerebrum (Żernicki 1964, Żernicki and Dreher 1965, Żernicki et al. 1967) [1].

8. Reversible decortication (Teitelbaum and Cytawa 1965, 1967, Narębski and Przybyłek 1966, Małecki et al. 1966, [9, 11, 22].

9. The effect of elevated temperature on the central nervous system (Gwóźdź 1966, Krause and Gwóźdź 1965) [16].

10. EEG activity in the anaphylactic shock (Narębski 1965, Narębski et al. 1966) [9].

11. Central control of respiration (Karczewski 1964, Czarnecka 1966, Karczewski et al. 1966, Przybylski 1966) [4].

III. PHYSIOLOGY OF SPINAL CORD

1. Variability of spinal reflexes (Afelt 1965, Afelt and Jankowski 1965, Jankowski 1965, Kozak and Westerman 1966) [1].

2. Pyramidal and extrapyramidal influences on spinal cord activity (Hammer et al. 1966, Hongo et al. 1966, Jankowska and Tarnecki 1965, Hongo and Jankowska 1967) [1].

IV. PHYSIOLOGY OF PERIPHERAL NERVOUS SYSTEM

1. Neuro-muscular and ganglionic transmission (Kostowski 1965, Janiszewski 1965, Filczewski et al. 1966, Gawęcka and Kostowski 1966, Janiszewski and Skubalanka 1966, Kostowski and Gumułka 1966) [9, 13, 22].

2. Movements of axoplasm in normal and regenerating nerve fibres (Lubińska 1964, 1965 [1, 2].

3. Trophic influences of the nerves on muscles in young animals (Lubińska and Zelena 1966a) [1].

4. The system of acetylcholinesterase in the nerve fibers (Lubińska et al. 1964, Lubińska and Zelena 1966b) [1, 2].

5. Regeneration of nerves (Koczocik-Przedpelska 1964, Koczocik-Przedpelska and Bombicki 1966) [19].

NEUROPHYSIOLOGICAL AND RELATED LABORATORIES IN POLAND

(the heads of laboratories are indicated)

POLISH ACADEMY OF SCIENCES

1. Department of Neurophysiology, the Nencki Institute of Experimental Biology, Warsaw 22, Pasteura 3 (J. Konorski):
   Laboratory of Neurobiology (L. Lubińska)
   Laboratory of Neuroanatomy (vacant)
   Laboratory on Isolated Cerebrum (B. Żernicki)
   Laboratory on Sensory Systems (W. Kozak)
   Laboratory on Spinal Cord (E. Jankowska)
   Laboratory on Classical Conditioning (K. Zieliński)
   Laboratory on Instrumental Conditioning (S. Sołtysik)
   Laboratory of Functional Organization of Subcortical Systems (vacant)
   Laboratory of Functional organization of the Limbic system (E. Fonberg)
   Laboratory of Functional Organization of the Neocortex (J. Konorski).
2. Laboratory of Neurochemistry, Department of Biochemistry, Nencki Institute of Experimental Biology, Warsaw 22, Pasteura 3 (S. Niemierko).
3. Department of Physiology of Work, Warsaw, Jazgarzewska 1 (S. Kozłowski).
4. Laboratory of Electrophysiology, Experimental Pathology Center, Warsaw, Dworkowa 3 (W. Karczewski).
5. Laboratory of Bionics, Institute of Automatics, Warsaw, Krajowej Rady Narodowej 55 (R. Gawroński).
6. Department of Neurosurgery, Warsaw, Białobrzeska 58, (L. Stępień).
7. Neuroendocrinological Laboratory, Institute of Animal Physiology and Nutrition, Jabłonna near Warsaw (E. Domański).
8. Laboratory of Neuropharmacology, Institute of Pharmacology, Cracow, Grzegórzecka 16 (J. Hano).

UNIVERSITIES

9. Chair of Neurophysiology and Comparative Physiology, Nicolas Copernicus University, Toruń, Mickiewicza 24 (L. Janiszewski):
   Department of Neurophysiology (S. Narębski)
   Department of Comparative Physiology (L. Janiszewski).
10. Department of Animal Physiology, University of Łódź, Łódź, Rewolucji 1905 r. 66 (A. Romaniuk).
11. Department of Animal Physiology, Curie-Skłodowskiej University, Lublin, Akademicka 12 (J. Cytawa).
12. Department of Comparative Neuroanatomy, Jagiellonian University, Cracow, Krupnicza 50 (J. Kreiner).

SCHOOLS OF MEDICINE

13. Department of Experimental Pharmacology, School of Medicine in Warsaw, Warsaw, Krakowskie Przedmieście 26/28 (P. Kubikowski).
14. Department of Neurology, School of Medicine in Warsaw, Warsaw, Oczki 6 (J. Hausmanowa-Petrusewicz).
15. Department of Psychiatry, School of Medicine in Warsaw, Warsaw, Nowowiejska 27 (A. Jus).
16. Department of Physiology, Silesian School of Medicine, Zabrze 8 — Rokitnica (M. Krause).
17. Department of Pharmacology, Silesian School of Medicine, Zabrze 8 — Rokitnica (T. Chruściel).
18. Department of Physiology, School of Medicine in Łódź, Łódź, Lindleya 3 (W. Traczyk).
19. Department of Physiology, School of Medicine in Poznań, Poznań, Święcickiego 6 (J. Kiersz).
20. Department of Anatomy, School of Medicine in Gdańsk, Gdańsk, Al. Zwycięstwa 41/42 (O. Narkiewicz).
21. Department of Physiological Chemistry, School of Medicine in Lublin, Lublin, Lubartowska 85 (T. Borkowski).

OTHERS

22. Department of Pharmacology, Institute of Pharmacy, Warsaw, Rydygiera 8 (I. Małecki).

23. Department of Physiopathology, Institute of Haematology, Warsaw, Chocimska 5 (J. Panasewicz).
24. Laboratory of Physiology of the Nervous System, Institute of Psychoneurology, Pruszków, Partyzantów 65 (S. Sołtysik).

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ON THE ROLE OF RELATIONS BETWEEN LANDMARKS AND THE NEST-HOLE IN THE PROXIMATE ORIENTATION OF FEMALE *BEMBEX ROSTRATA* (Linné) (*Hymenoptera, Sphegidae*)

J. A. CHMURZYŃSKI

Department of Biology, The Nencki Institute of Experimental Biology,
Warsaw 22, Poland

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The spatial orientation[1] of flying aculeate *Hymenoptera* is based on their remembrance of perceived cues that serve them for navigation. Enhancing our knowledge of this mechanism requires, therefore, on the one hand, studies on the problem of learning and memory in these insects and, on the other, dealing with the problem of stimuli and perception processes which play a considerable role. The latter problem is the object of our interest.

It is clear from the investigations on the recognition of the environment of their nest by the insects that in the psyche[2] of these animals — when their perceptive capabilities are examined — there exist contradictory and conflicting tendencies to base their activities, during the orientation process, on both the individual elements of the environment and, on the other hand, on relative characteristics combining these ele-

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[1] In the present paper, the term "spatial orientation" is meant as a synonym of homing, that is, the capability, mechanism, as well as the process itself of finding and identification of the way and place.

[2] By the term "animal psyche" I mean an assemblage of dispositions and nervous processes, manifested in an animal's behaviour, as, for instance, instincts, taxes, temperament, motoric and vocalisation patterns, etc., capability to form acquired behaviour patterns and learning dispositions, as well as behaviour patterns already developed and an animal's content of memory, capability of plastic behaviour, etc. which virtually may be objectively studied by a method of observation and experiment, combined with critical conclusions drawn on such a basis.

ments with each other. It is not only the spatial relation between the target and the perceived elements of its environment — many of them being usually considered simultaneously — that are evaluated by an insect but, moreover, it takes into account spatial relations, occurring between all these elements, as well as their configuration.

For the sake of accuracy, it should be stated that these tendencies play a certain role even at a lower level, i.e. in the stage, in which animals perceive particular landmarks — in which they have to do with both single modalities and qualities (as, size shape, colour, smell, etc.) as well as with a whole assemblage they form.

Under natural conditions, both these tendencies — analytic and syncretistic — constituting two aspects of the perceptic process, cooperate with each other and mutually supplement themselves. However, they may be artificially separated during the experiments such as, for instance, studies on the hierarchy of impressions in spatial orientation (cf. Chmurzyński 1953, 1957, 1960, Tinbergen and Kruyt 1938).

According to Baerends (1941), the landmarks are used as an entirety by *Ammophila pubescens Curt.*[3] in both its distant and proximate[4] orientation. However, under certain circumstances, he succeeded in training this wasp to respond to a single cue (a black cylinder 5 cm high and 5 cm in diameter). A typical choice between a complex landmark, that is, an excavation in a wall in which the nest-hole was situated and a near landmark, i.e., a tuft of orpine (*Sedum*), displaced during an experiment with another thread-waisted wasp, *Ammophila heydeni* Dahlb., has been described by Rabaud (1919). As usually with a reference system rich in details (in this case, excavation in a wall), the change in the position of one element caused only a prolonged duration of the recognition flight and did not evoke any significant confusion of the wasp.

A considerable capability to avail itself of small landmarks of the nest-hole environment, visually perceived, is displayed in its complex orientation by a related species, *Sphex albisectus* Lep. It is manifested, for instance, by the fact that it is only with difficulties that it finds its nest-hole — and when it happens it is mostly by accident — when in its

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[3] A form examined in the work by Baerends (1941) and called by him *A. campestris* Jur. has been assigned by Olberg (1959, p. 12) to this species.

[4] On the basis of Rabaud's (1927) division, the stage of *proximate orientation* has been characterized (Chmurzyński 1963, 1964a,b) as a stage in which a vicinity of the nest is recognized by the animal. The field of proximate orientation is, therefore, surrounded by the field of *distant orientation* within which a vicinity of the nest is looked for and found by the animal. The field of proximate orientation surrounds in turn a tiny field within which the nest itself or its entrance is found by the animal by means of mechanisms peculiar to the *immediate orientation.*

absence the terrain around the entrance was swept clean with a twig (Benz 1959, p. 313).

The papers by Tinbergen and Kruyt (1938) and by van Beusekom (1948) have irrefutably proved that conditions similar to those, observed in *Ammophilae,* also exist in the spatial orientation of bee-wolf, *Philanthus triangulum* (F.). The results described in the latter work will be more than once extensively referred to in other parts of the present paper. Here, it may be mentioned that the former two authors recorded the bee-wolf's complex orientation, based on a twig, two tufts of grass *Corynephorus canescens* (L.) and three pine cones which was revealed after the displacement of some of these landmarks.

A complex use of landmarks has been found by van Iersel (1952) in common sand wasp's proximate orientation. Sometimes, a considerable role is played by object, seen on the horizon (van Iersel and van den Assem 1964). The same has been noted by Tsuneki (1956) in the case of a related species of Japanese sand wasp, *Bembex niponica* Smith. This author believes that distant landmarks are to a considerable extent used by Japanese sand wasp. A similar conclusion has been reached by Marchand (1900) after his experiments on *Bembex rostrata* (L.).

There is no need to remind that, in their proximate orientation, all these species of digger wasps (*Sphegidae s. Sphecidae*), as well as bumblebees (*Bombinae*), studied by Wagner (1907), control their flight by beacons and not by stimuli, coming from the nest-hole itself (cf. Marquenie 1954).

In the present paper we shall reflect upon various aspects of the fact that the female *Bembex rostrata* (L.) base their spatial orientation on spatial relations. Some attention will be paid to the correlation between the role of landmarks and their distance from the nest-hole, as well as to their situation in relation to the nest entrance. We shall also deal with the problem of distance estimation by *Bembex* which is of a considerable importance to the accuracy of proximate orientation. More closely, we shall examine the perception of the landmark configuration as a whole, that is "gestalt". Nowadays — in particular after van Beusekom's (1948) special elaboration of this problem — nobody can doubt that the assemblage of landmarks affects the hymenopteron as an integrated whole and is perceived by it as what is called gestalt, used in a similar sense as that of a term, coined by the representatives of the school of Gestalt-psychology: Ehrenfels (1890), Koffka (1915, 1922), Wertheimer (1922—1923) [cf. Biryukov 1959; Carthy 1954; Dembowski 1932, 1935, 1955; Hertz 1928, 1929, 1930, 1931, 1935; Köhler 1915, 1918]. (This is not necessarily synonymous with accepting the entire theoretical concept of the Gestalt-psychology). Thus, the question arises whether or not *Bembex*' perception is, or happens to be configurational in character. In particular it is interesting whether an assemblage of landmarks is perceived by the wasp as a gestalt, i.e. a specific integrity of particular components and relations between them, and whether this gestalt may be subject to transposition.

MATERIAL AND METHODS

The experiments have been carried out in 1954, 1955 and 1960 south of Warsaw in the neighbourhood of the localities Skolimów-Konstancin and Chylice, as well as, in 1962, at Świder near Otwock.

Female common sand wasp, *Bembex rostrata* (Linné 1758) constituted subject of experiments. Twenty five individuals[5] were used for experiments, included in the scope of this work.

These field experiments were carried out near the nest-holes of the individuals investigated. Their tendency to return to the nests containing eggs or larvae, was used. Depending on the problem, tests of a few types were formed.

The first group of experiments consisted in making use of natural temporal connections in animals' behaviour. Here belonged the studies on the role of particular components of the nest-hole environment in proximate orientation. In the experiments of this kind, which for a long time have been used by students of insect behaviour (cf. Bouvier 1900, 1901; Fabre 1879, 1882; Marchand 1900), the natural landmarks were removed or the new ones added.

The type of experiments, what I termed "disturbance experiments" were based on the observation of disturbance, evoked in the animal's behaviour by an artificial change in the vicinity of the nest or concerning the nest-hole itself. This method has been similarly developed in the 1950's by two scientists, van Iersel (1952) and the present writer (cf. Chmurzyński 1959), both experimenting independently one from the other. If the technique of van Iersel is based on the measurement of time of the orientation flight, i.e. pre-leaving flight (k), called by him "re-orientation time" (ROT), the present author's method consists in comparing the time (measured in seconds) of the recognition flight, i.e. pre-entering flight (g), performed by the insect after discovering changes that took place near its nest entrance (and which each time were removed by the experimenter after the insect has entered the nest-hole) with the mean time of a normal recognition flight of this individual near the same nest (g_0). Several modification were also applied to this method. In these experiments, a flight of the returning animal from the moment it appeared in the vicinity of the nest-hole, that is, after it crossed the boundary of a field with a radius of about 2 m to the moment it alighted in this field was considered a recognition flight. The quotient of a disturbance of the recognition flight,

$$i_g = \frac{g}{g_0}$$

was assumed as an expression of, among other things, the intensity of a change which disturbed the animal's orientation. The value g_0 is measured for a given individual near a given nest and, if practicable, expressed in the form of a mean

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[5] They are marked by symbol B with ordinal numbers.

value of a few measurements. The lowest value, assumed for calculating reasons, was 1 sec (the values lower than 0.8 sec. are seldom met with). The results of $i_g = 3$ and more are considered significant figures. The disturbance method is marked by a certain important property which consists in the fact that the response of the animal to the change introduced is not directly proportional to the disturbance intensity of, for instance, an object, placed near the nest-hole, but it expresses the change in the entire configuration (gestalt) of the nest-site which is produced by this new element against the background of all landmarks existing so far. This method, like that of the quotient of the recognition flight disturbance, i_k, is very useful in all cases in which it is necessary to find whether a given stimulus has been noticed at all by the animal.

The second group of experiments consists of those during which animals are trained. The simplest of them, "displacement experiments", consist in provoking the animal to fly to the landmarks, moved from the nest-hole environment to a certain distance (or turned by a certain angle around the vertical axis of the system of landmarks). It was necessary of course for the animal to get accustomed to these landmarks prior to the experiment and to associate them with the nest either as a natural element or that, introduced by the experimenter. Experiments of this type were successfully performed on *Bembex* wasp as early as 1900 (Bouvier, 1900).

The "training-choice experiments" constitute the next stage in the development of the experiments of this type. Their purpose is to establish the importance of different environment features to the spatial orientation of the animal. After a training to recognize an assemblage of two types of landmarks situated near the nest-hole, when the wasp was absent from the nest, they were placed separately in two sets. The landmark sets were so oriented to the flight direction of the returning animal that one of the assemblages was found by it on the left and another on the right side of the nest entrance. In this experiment, it was found that the female *Bembex rostrata* (L.) did not approach into the wind like bee-killer wasps, *Philanthus triangulum* (F.) but they flew to the nest entrance whose opening was inclined to the perpendicular (Fig. 1). The results of the experiments were recorded in a table of the wasps arrivals in both assemblages of the experimental system. The animal had to choose many times since, driven away by the experimenter to a sufficient distance, it was compelled to choose one of the landmark sets again. The experiment was considered a success when, after reaching positive results of training, sufficient data concerning an insect's arrivals in the experimental assemblages were obtained. Thus, the cases were disregarded in which the wasp kept arriving only in a true

Fig. 1. *Bembex's* approaching the nest entrance: recognition flight. Wind direction indicated by arrows

nest-hole despite the fact that no experimental landmarks were placed in its vicinity. The ratio of the numbers of the wasp's arrivals in the nest at the one side of the set of landmark to the arrivals at the other side indicated a relative importance (="hierarchy") of modalities and qualities, represented by each of these assemblages, to the spatial orientation. It was considered that the wasp prefers certain landmarks to others when the significance level of the ratio was $p \leqslant 0.025$. In addition to these arrivals, certain cases were recorded of abortive alighting of the wasps at some distance from the target but only in the experimental field (that is, within a radius of 2 m and less from the true nest entrance), or near the proper nest-hole. This enabled the estimation of the orientation value of definite landmarks as compared with the natural environment of the nest-hole.

In the experiments the aim of which was to study average features of the common sand wasp, *Bembex rostrata* (L.), i.e. in the training-choice experiments, efforts were made to assure a greater degree of reliability of results which was attained by examining several individuals; data were based on the observation of at least 3 individuals. When, following the lack of material, certain deviations from these principles were necessary, the results of other experiments, similar in character, were taken into account to support the test. [Sometimes, it was necessary to refer to the experiments described in other publications by the present writer (cf. Chmurzyński 1953, 1960)]. This may be justified by a small number of the available individuals. The selection of nests situated in a terrain, preferably devoid of grassy vegetation and numerous other natural landmarks, was necessary for the experiments which constituted a documentary evidence of the present paper. For this reason, sometimes, one individual was used for several experiments.

RESULTS

1. Distance relations and quantity of landmarks

The first series of experiments was devoted to the problem of accuracy in perceiving distance relations by *Bembex rostrata* (L.), that is, to the capability which, in the studied stage of orientation, is decisive for the precision of proximate orientation and determines the area of the immediate orientation field (cf. Chmurzyński 1964a).

Test 1 consisted in training the wasp to respond to a visual figurative stimulus in the form of a pine twig, lying close to the nest-hole and, hereafter — in the animal's absence — in shifting this twing and turning it around the vertical axis. After the return of the wasp, its behaviour was observed in the neighbourhood of the nest. This experiment was performed on five individuals whose nests were situated in an area relatively devoid of natural landmarks.

Here is an excerpt from the record of such an experiment, performed on B_{33} (cf. Chmurzyński 1959, 1964a).

Konstancin, June 23, 1954. Hard, sandy path across a clearing near a playground. Broken cloud[6]; temperature 28°C, later on, 30°C; moderate breeze from WSW.

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[6] For the sake of clarity and simplification, the cloudiness is determined

2^{22} p.m.[7] B_{83} is inside the nest-hole;
a pine twig 42 cm long and 40 cm wide (Fig. 2a) was placed near the nest-hole.
Bembex emerged from the nest-hole, digging up the sand, took off two times for a few cm above the ground, hereafter, remained hovering over the entrance [cf. van Iersel and van den Assem 1964, Fig. 3 d(1)] for a certain time and, returned to the nesthole,
2^{26} p.m. stoped the entrance with sand from the inside;
2^{29} p.m. no change.
Observation suspended.

The same place, June 24, 1954. Broken clouds—cumulus; temperature, 27°C; gentle breeze from WNW.

10^{39} a.m. B_{83}'s nest-hole open; twig in the same position; B_{83} came back,
11^{04} a.m. entrance closed from the outside.
I removed a yellow sand, thrown by the wasp out of the canal and chamber of the nest-hole.
12^{34} p.m. B_{83} came without a prey, alighted close to the entrance and dug the sand,
12^{41} p.m. continued to dig...,
12^{44} p.m. entered the nest, stopped it with sand from the inside.
Observation suspended.

The same place, June 25, 1954. Clear sky — cumulus; temperature 28°C; light breeze from WNW.

11^{20} a.m. B_{83} is away from the nest,
11^{21} a.m. returned (without a prey), came directly to the nest, turned, flew around the twig, alighted, uncovered the canal, entered the nest and stopped it from the inside,
12^{56} p.m. went out, closed the nest entrance, made an orientation flight ($k = 2\cdot0$ sec) and flew away,
12^{57} p.m. returned, alighted, dug the sand (for 10 sec), entered the nest-hole, stopped it,
1^{07} p.m. left the nest, closed the entrance, dug for a while, once more stopped the entrance, flew away without an orientation flight (i.e., $k = 1\cdot0$ sec).
1^{10} p.m. I shifted the twig somewhat nearer the nest-hole (Fig. 2b).
B_{83} arrived without a prey, made a recognition flight, alighted (Table I).

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according to a four-grade scale for which the following designations are used: clear — 0—$^{1}/_{4}$ cloud cover of the sky; scattered cloud, $^{1}/_{4}$—$^{1}/_{2}$ cloud cover; broken clouds, $^{1}/_{2}$—$^{9}/_{10}$; and overcast, $^{4}/_{4}$. Temperature was measured by means of a shaded thermometer at an elevation of about 1·5 m above the ground of the observation area. Wind force was determined according to the Beaufort International Scale of Wind Force with the following verbal equivalents of figures: 0° — calm (wind velocity, 0—0·5 m/sec), 1° — light air (0·6—1·7 m/sec), 2° — light breeze (1·8—3·3 m/sec), 3° — gentle breeze (3·4—5·2 m/sec), 4° — moderate breeze (5·3—7·4 m/sec), 5° — fresh breeze (7·5—9·8 m/sec), 6° — strong breeze (9·9—12·4 m/sec), etc. (Critchfield 1960, p. 48).

[7] Local time of 21° East. longit, used throughout the present paper, differing by + 24 minutes from the proper Central European Time, that is, without consideration of the summer time, introduced in Poland in summers of 1957—1964.

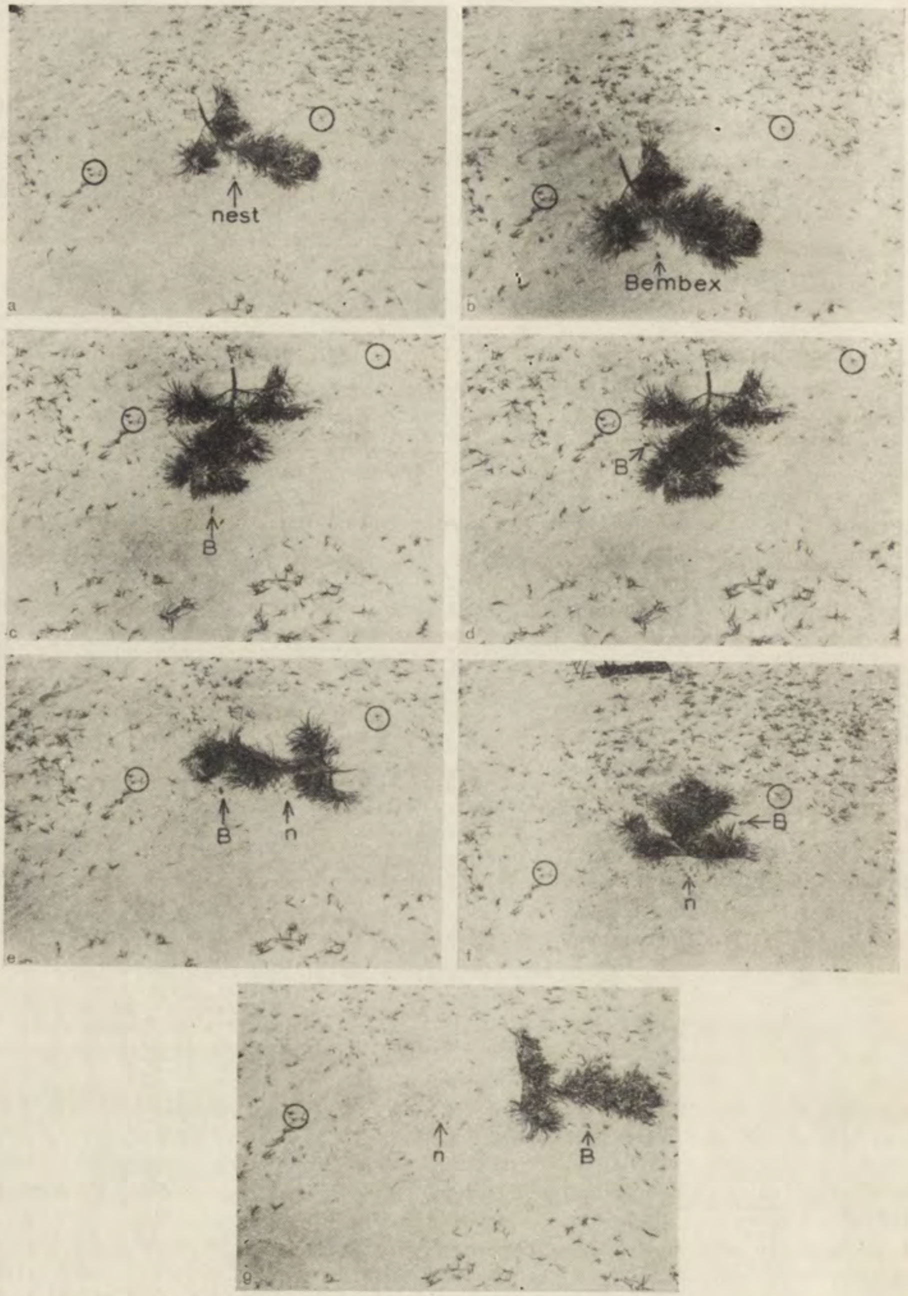

Fig. 2. A series of photographs of test 1 with B_{83} on June 23—25, 1954, showing the precision of visual gestalt: *a* — training system with nest-hole visible between branches of a pine twig; the remaining photographs (*b* — *g*), taken from the same direction, depict the displacements and changes in the position of the twig by 90°, 180°, 270° and 360° in relation to the nest (n), as well as the behaviour of *Bembex* (B). To aid the reader's observation, two tufts of grass are surrounded by circles

Table I

Frequency of choice		
Sham nest entrance	True nest entrance	Abortive alighting
3	0	1

I turned the twig about by 90°.
The wasp returned without a prey and for about 2 min (*g*) at first hovered parallel to the axis of the proper nest entrance (Fig. 2c), then, alighted in a place which was identically situated in relation to the twig as the true nest-hole was in the training system of landmarks (Fig. 2d); frightened away, it returned and 8 times alighted in this place.
I frightened the wasp away and again turned the twig by 90°, so that now, the nest-hole was situated in front of the twig, much the same as in the training system.
B_{83} came (without a prey) and alighted as in Table II.

Table II

Frequency of choice			
Sham nest entrance	Place X	True nest entrance	Abortive alighting
0	6	1	2

It should be mentioned that, in this case, it flew away from the true nest entrance without being scared away. (By the "sham nest entrance", I mean a place identically situated in relation to the twig as the true nest-hole was in the training system; "place *X*" is a place where B_{83} dug the sand at the moment when the photography was taken —Fig. 2e); I scared the wasp away and once more turned the twig by 90° Fig. 2f); B_{83} came without a prey and alighted 14 times (Table III);

Table III

Frequency of choice		
Sham nest entrance	True nest-hole	Abortive alighting
13	1	0

I scared the wasp away and once more turned the twig by 90° so that now it was situated parallel to the training system position and the "sham nest entrance" — 30 cm to the right from the nest-hole (Fig. 2g);

> B_{83}, arriving without a prey, 11 times alighted close to the sham nest entrance [...].

In experiments with B_{220}, the twig was placed at angles, 90°, 180° and, once more, 90° in relation to the training system position. Each time, the wasp dug the sand in a place identically situated in relation to the twig.

In the cases in which wasps dug in places identically situated in relation to the twig, there was a great degree of their accuracy which determined the field of immediate orientation about 2.5 cm in diameter. More or less the same results were obtained in other experiments, that is, under natural conditions the diameter did not exceed 3·5 cm (i.e. about 9·5 sq cm in area — cf. Chmurzyński 1959, 1964a). There are reasons to believe that *Bembex* is marked by the capability of an exact estimation of distance in which, may be, a certain role is played by its binocular vision (cf. Chmurzyński 1964 c, Zänkert 1939).

In subsequent cases, wasps displayed a more pronounced tendency to keep the same orientation of their body position in space as that during training experiments. The following excerpts from the record of an experiment with B_{88} may serve as an example.

Konstancin, July 6, 1954. Sandy path across a clearing near the playground. Clear sky, few cumulus type clouds; temperature, 23° C; light breeze from SSE.

After training B_{88} to orient its flight by a pine twig lying near the nest-hole similar to the previous case (Fig. 3a).

Fig. 3. Test 1 with B_{88} on July 6, 1954: *a* — training system (continuous line marks the nest entrance), *b* and *c* — experimental systems (dotted lines — sham nests, position of *Bembex* digging in places *x*, *y* and *z* — indicated by arrows)

11^{56} a.m. the twig was placed 2 m to the right from the nest entrance.
B_{88} returned without a prey, dug into the sham nest entrance near the twig.
The twig was turned, in the same place, by about 120° to the right (Fig. 3b).

Scared away, B_{88} returned and alighting in place x, on the right side of the twig, resumed digging;

the wasp was scared away and the position of the twig changed by a turn to the right by additional 150° (Fig. 3c);

B_{88} returned, dug into the supposed nest-hole — y, after being scared away and returning, dug in place y 2 times, then went to the left side of the twig and dug in place z and, then, once more returned to place y.

12^{02} p.m. Landmarks removed [...].

Fig. 4 depicts the results of an analogous experiment with B_{221}, carried out on July 17, 1962. The experimental system was placed 25 cm to the right from the nest entrance. The position of the alighting wasp is indicated by tiny arrows and number of the animal's returns to this same place — by figures, accompanying the arrows. The experiment was performed between 1^{39} and 2^{54} p.m. with clear sky (a few clouds of the cirrus, cirro-stratus, cirro-cumulus and cumulus type) at a temperature of 24°C and moderate breeze from NW.

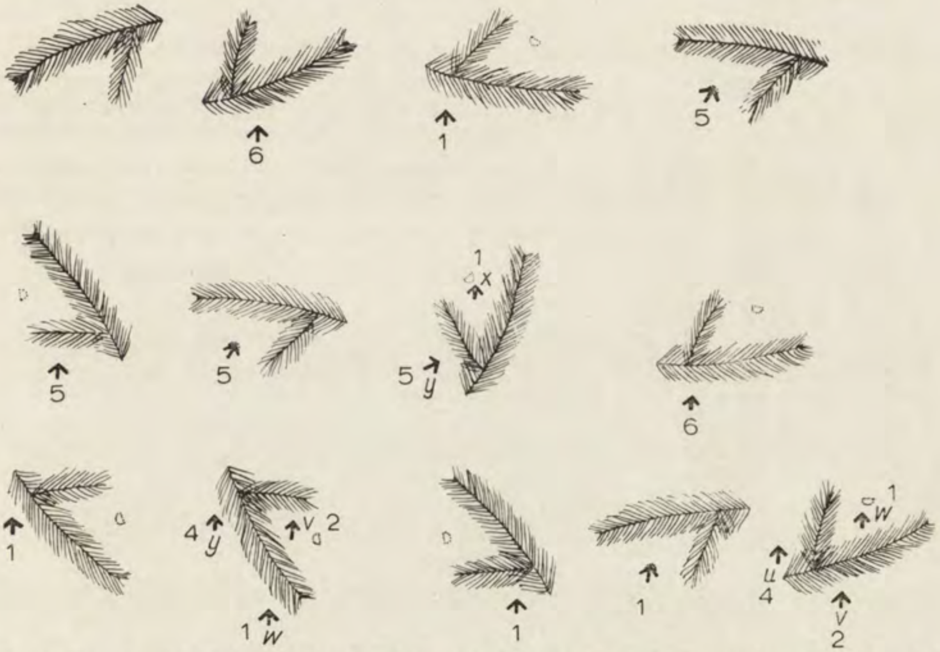

Fig. 4. Test 1 with B_{221} on July 17, 1962: training system and successive experimental systems. Explained in text

Under much the same meteorological conditions, on July 28, 1962 between 1^{53} and 2^{04} p.m. and on August 8, 1962 between 2^{25} and 2^{39} p.m., with the experimental system turned by 90°, 180° and 270°, B_{228} alighted as indicated with arrows in Fig. 5.

Test 2, opening the second series of experiments, was a further step towards the estimation of a role, played in the accuracy of proximate orientation by an increased number of landmarks. It was carried out with B_{220} on July 19, 1962 between 3^{34} and 4^{54} p.m. on a calm and warm day. After training the wasp to orient itself by two black sheet iron plates, one of them 4 cm wide and 20 cm long and the other 4 cm high and 20 cm long, driven vertically in the ground, the plates were separately disposed on both sides of the nesthole. The results are shown in the Table IV (R — means that this system was situated to the right from the nest-hole, L — to the left; letters x and y, accompanying numbers which express frequency of choice of a given system, determine the place in which the wasp alighted as indicated in the table headline, position x corresponding to the situation of the nest-hole within the training system).

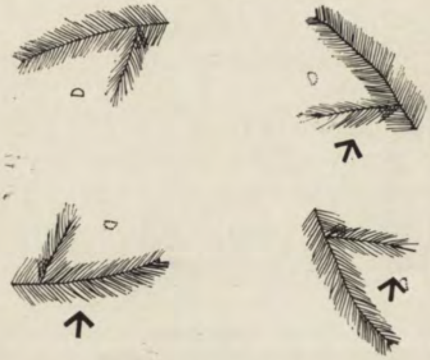

Fig. 5. Test I with B_{228} on July 28 and August 8, 1962: training system and successive experimental systems. Explained in text

Table IV

Frequency of choice				
$y^{\cdot} / .x$		$x \cdot \diagdown \cdot y$		
L	$8x$	R		$2y$
R	0	L	$8x$,	$2y$
L	$4x$	R	$4x$,	$2y$
R	0	L	$9x$,	$1y$
L	$2x$	R		$8y$
R	0	L	$8x$,	$2y$
L	0	R	$2x$,	$8y$
	$14x$		$31x$,	$25y$

The wasp came 3 times to the nest-hole.

More data were supplied by *test 3,* carried out with B_{81}. Here are some excerpts from the record:

Konstancin, June 25, 1954. Field path crossing a clearing near the playground. Clear — a few cumulus type clouds; temperature 28°C; light breeze from NW.

A female *Bembex rostrata* (L.) B_{81} was absent from the nest near which, since 12^{40} p.m. on June 22, 1954, a small stone ($4 \times 4 \cdot 5$ cm) has been lying (Fig. 6 : I; n — nest);

11^{43} a.m. I shifted the stone 10 cm backwards (Fig. 6: II).

12^{12} p.m. B_{81} came with a fly, $g = 1$ sec (no response to the changed position of the stone), dug in sand, entered the nest.

I put the stone in its previous place;

12^{14} p.m. B_{81} came out, stopped the nest-hole, took off and flew a few orientation curves: $k = 4$ sec, alighted nearby, once more $k = 15$ sec (the orientation effect of shifting the stone was thus revealed: $i_k = 19$); the wasp flew away.

I removed a grass blade, marked *Q* in Fig. 6, and put the stone in its previous place [...].

Fig. 6. Test 3 with B_{81} on June 25—26 1954. Explained in text

The same place, June 26, 1954. Clear, a few fracto-cumuli; temperature 28°C; light breeze from WNW.

11^{02} a.m. I smoothed the sand near the nest;

11^{03} a.m. B_{81} came, carrying a caught fly, $g = 2 \cdot 5$ sec (zigzag flight), alighted, dug, entered the nest,

11^{09} a.m. went out, closed the nest entrance and departed in a slow, straight-line fight, $k = 2$ sec.

I shifted the stone 25 cm backwards (Fig. 6: III);

11^{18} a.m. B_{81} came with a prey, $g = 4$ sec (first it approached the stone), alighted on the nest, dug, entered the nest.

To reinforce the training, once more, I put the stone in its previous place; the wasp emerged from the nest, closed the entrance, $k = 2$ sec, flew away.

To make sure about the role played by other landmarks near the nest, I tore out all adjacent grass blades so that the stone remained as the only landmark.

11^{34} a.m. B_{81} came with a prey, $g = 5$ sec (i_g significant), dug, entered the nest, after 20 sec emerged once more, for 32 sec stopped the nest-hole, but directly flew away without any zigzags of orientation flight which seemed to indicate its habituation to the changes, occurring close to its nest.

11^{36} a.m. To appraise the orientation role of the stone, I took it away; small holes which remained after closing the nest were now the only landmarks.

11^{50} a.m. B_{81} came flying up with a prey, took a recognition flight, repeatedly approaching grass blades about 0·4 m to the right from the nest (cf. Fig. 6) and, in addition, hovered around within a radius of 1·5 m over the nest environment where, at 11^{02} a.m., the sand has been smoothed — $g = 2$ min 7 sec, alighted, dug (10 sec), entered the nest entrance.

Once more I put the stone near the nest;

11^{54} a.m. B_{31} came out, closed the nest-hole, made an orientation flight ($k =$ 23 sec) and departed.

Since one might assume that, after all, in this situation, the small holes near the nest entrance constituted certain landmarks (cf. Chmurzyński 1964a), I filled them with sand and, as at 11^{09} a.m. (position III), once more shifted the stone by 25 cm to check — under changed conditions — its role as the then only landmark.

11^{57} a.m. B_{81} arrived without a prey, $g = 3$ sec, alighted near the stone (!), $k =$ 7 sec and flew away.

12^{01} p.m. I moved the stone in the same direction about 50 cm from the nest (Fig. 6 : IV).

12^{06} p.m. The wasp came without a prey, flew around the system for a certain time, departed,

12^{21} p.m. returned, $g = 7$ sec, alighted near the stone, took off again and flew away, following a straight-line course without orientation curves. This proved that the animal did not noticed any changes. It was due to the fact that it had to do with an only essential landmark in this monotonous environment and thus it had not a "sensation of being confused". If it did feel such a sensation, this would be behaviourally expressed by an orientation or recognition flight longer than that it actually made.

12^{25} p.m. I moved the stones 25 cm to the left from the nest-hole (Fig. 6 : V).

12^{32} p.m. B_{81} came with a prey, $g = 4$ sec, alighted and dug close to the stone.

I shifted the stone to its previous place near the nest; the wasp promptly approached the proper place, dug up the nest-hole and entered it,

12^{33} p.m. emerged from the nest-hole, closed it, $k = 2$ sec and flew away [...].

It is clear from this series of experiments that the female *Bembex rostrata* (L.) recognizing the environment of her nest entrance, displays the tendency to base her orientation on a sufficient number of landmarks, primarily those distributed over the field of proximate orientation, i.e. within a radius of, at most, 4 m (Chmurzyński 1959, 1963, 1964a,b) and not on one or two components, selected from the whole set of them. The indication was also obtained from this series that it was not a question of remembering only characteristic features common for the components of the landmark system. Test 3 included landmarks that differed from each other in such qualities as, shape, degree of contour "richness", intensity of contrast between a given landmark and its environment, colour, etc. To a considerable extent, the thing was to remember the whole of relations between particular components of the nest-hole environment. A change introduced in some of them, causing a change in the configuration as a whole, evoked a clearly visible confusion in the wasp's behaviour.

We are aware that, in *Bembex rostrata* (L.) it is accompanied by a good knowledge of single landmarks which — as often observed — are differently used for orientation which is due to their various characters, i.e. what is called, hierarchy of impressions. In the hierarchy of senses (modalities), vision is the most important sense, governing this wasp's movements. The studies on the hierarchy of visual qualities revealed an important role played in its proximate orientation by : large, three-dimensional landmarks, those which cast shadows, those having a broken pattern, and those having a "rich" contour (the latter applies mainly to flat landmarks with a high quotient of the contour length divided by the area of a figure) Chmurzyński 1953, 1957, 1960, 1966; cf. van Iersel and van den Assem 1964 — discussion).

The significance of these tendencies in common sand wasp, *Bembex rostrata* (L.) in a natural situation similar to that in test 3, is visualised in *test 4*. Its aim was to establish a mutual hierarchy of a stone and either a pine cone or a pine twig, that is, objects which are often met with near the nests of *Bembex rostrata* (L.), insects living in the vicinity of coniferous forests (cf. Bouvier 1901, Chmurzyński 1953, 1965a, Olberg 1959, Vuchetich 1927).

In the training system, the cone and the stone were lying 8 cm apart on both sides of the nest entrance. In the experimental system, this distance amounted to 40 cm. B_{94} preferred the cone to the stone in the ratio of 15 : 0 ($p = 0{\cdot}01$). The stone may, however, predominate over the cone (in B_{90}, in the ratio of 12 : 1) if it is of a sufficiently larger size.

In another experiment, the wasp could choose between a pine twig about 30 cm long and a stone about 10 cm in diameter, (after the removal of the twig, the wasp dug near the stone). B_{88} preferred the twig in the ratio of 5 : 0 ($p = 0{\cdot}025$).

In both cases, the wasps dug in an identical place, in relation to the landmark, with that in which the nest entrance was situated during the training, a proper distance being kept as observed in test 1.

The role played by distance relations in using landmarks was studied in a subsequent series of experiments. In *test 5*, after a training on 4 yellow cubes with sides 4 cm long and 4 larger ones, with sides 8 cm long, disposed at a double distance from the middle of the system as the previous ones, they were distributed separately (this test followed the lines of experiment 53 in the work by Tinbergen and Kruyt 1938). Results in the Table V.

Table V

Wasp	Frequency of choice	
	nearer	farther
B_{28}	15	0
B_{30}	7	0
B_{211}	9	1
	31	1

In *test 6*, the conspicousness of shape was opposed to the distance, i.e. 4 black, wooden cubes with the dimensions of 4×4×4 cm were opposed to 4 pine cones put at a double distance (about 24 cm) from the middle of the system. Results in the Table VI.

Table VI

Wasp	Frequency of choice			
	cones /nearer/	cubes /farther/	nest-hole	abortive alighting
B_{59}	17	0	—	—
B_{64}	5	27	0	2
B_{70}	0	14	0	0
B_{71}	1	21	0	3
B_{73}	0	24	0	1
B_{74}	0	33	2	2
	23	119		

It is clear from the result shown above that the greatest role is played in the proximate orientation by landmarks, situated nearer the middle of the system and even those so articulated as cones, situated farther, are — in this respect — inferior to them (cf. Chmurzyński, 1966).

2. Position in relation to the nest entrance

In our experiments, we were also interested whether or not using elements of the nest environment by females of *Bembex* may depend not only on their mutual hierarchy, based on modalities and qualities, or on their distance from the nest-hole, but also on their position in relation to the nest entrance.

This problem was not especially examined. Instead, the results were available of observations, collected during other experiments.

Sometimes, during the training, the wasp happens to fly away outside the training system and, thereafter, seems to be unable to cross this "magic circle" and to alight within it on the nest entrance. Under such conditions, B_{220} tried to dig as close as possible but outside the system of four black cubes with a side 4 cm long. Likewise, in the case of an insufficiently memorized training system, sometimes, after the return to the nest, *Bembex* looks for it outside the system. In such a case, as with B_{191}, it is usually quite enough to remove part of the system of the entrance and the wasp comes within the area of the training system. Afterwards, the system may be completed step by step. Since the removal of a cube, situated behind the nest, usually does not produce such an effect, one may presume that frontal part of the system of landmarks, situated near the nest-hole plays, in the case of Bembex, a larger role in the proximate orientation than that, situated behind it. Nevertheless, I observed the tendency in a female *Bembex* to locate its nets so that there was a well-visible landmark behind the entrance (cf. van Iersel and van den Assem 1964 — discussion).

3. Configuration (gestalt)

After these introductory experiments, the role of the configuration in the proximate orientation of *Bembex rostrata* (L.) was dealt with.

The first series of experiments was devoted to the analysis of *a*) *the first property of gestalt*; "elements of configuration are subordinated to its whole".

At first, let us estimate to what an extent *Bembex rostrata* (L.) may tolerate the variability of the elements of the system of landmarks near its nest-hole.

Test **7.** In experiments in which B_{120} and B_{121} were trained on a black, convex ring, no visible disturbance was observed in g when the elements, forming this shape of "a black ring with the nest-hole inside", were substituted by a wreath consisting of black pine cones. However, it seems that individual tendencies may be considered in this case since an analogous substitution of a closed ring by a wreath of cones produced, in B_{76}, a significant increase in g which indicates the fact that these two types of systems were easily discriminated from each other by the wasp.

Test 8 was slightly different in character. In this case, the similarity of exchanged systems was not to manifest itself by a slight disturbance in the recognition flight (*g*) of the wasp, returning to its nest near which the system was placed, but by a successful *coming* of the animal to the system, situated a dozen or so cm from the nest-hole. This test was performed on B_{197} during an experimental choice. After a training of the wasp on a system of 6 black hemispheres ($r = 2$ cm) and 6 cylindrical blocks with equal area, alternately placed to form a wreath-like shape, a small, convex, black ring (21 cm in diameter) and a small, black, flat ring with an equal area were separately placed within the experimental system. After its arrival, the wasp made a recognition flight, 4 times alighted on the true nest entrance, 7 times dug in different places, flew over the systems, hesitated, hovering above them but never tried to alight among them. The differences proved to be larger than a possible similarity of the gestalt.

To extend the studies on this problem, *tests 9—13* were performed. They consisted in distributing — after the training on a given system — of an experimentary system which, in addition to old elements, known to the wasp from the training, also included other ones, contrasting with them. The results are shown in the table VII.

Table VII

No. of test	Wasp	Frequency of choice			
		Training landmarks	Neutral landmarks	Nest-hole	Abortive alighting
9	B_{168}	black stars 16	black crosses 17	18	35
10	B_{131}	normal pine cones 24	black hemispheres 0	5	5
11	B_{188}	black cubes 31	blue cubes 0	1	9
12	B_{136}	red cubes 5	black cubes 19	0	11
13	B_{54}	white discs 20	cream-yellow discs 5	—	—

They show that *Bembeces* are, on the whole, responsive to changes in the elements of configuration. This is manifested in tests 10, 11 and in — 13 in which the training colour undoubtedly predominated despite the fact that such a choice is rather against *Bembex'* natural preference (after the training with combination of both colours, the choice of white landmarks in the ratio of 36:78). In some cases, however, wasps displayed — in their behaviour — a configurational perception (tests 9, 12 and 13), the existence of which has already been indicated by test 7. The most easily tolerated by *Bembex* is the variability of "weak" landmarks, (i.e. those low-ranked in the hierarchy of visual qualities, such as, for instance, flat coloured discs) or a substitution of some elements by others, hierarchically more or less equivalent (test 12 in which, after the training on both systems of landmarks applied as a whole, the choice ratio amounted to 21:19 in favour of the red colour[8] (or by such landmarks which are difficult to discern (which may take place in the case of test 9; during the experiment on the hierarchy of these qualities, stars were preferred in the ratio of 23:15).

The significant role of colour in *Bembex'* gestalt perception is convincingly confirmed by *test 14* which is a continuation of test 11. After the training on four black cubes, they were easily discriminated by B_{188} in the experimental system from the blue ones. Moreover, when, after the removal of this system, another system was built of the same blue cubes, distributed 20 cm to the left from the nest-hole, the animal looked for the nest in different places without even trying to alight on this system. On the other hand, it was quite enough to substitute black for blue cubes to induce the wasp to dig (after being scared away — 8 times) in this system. A repeated exchange of black by blue cubes once more yielded a negative result and even — after placing blue cubes around the nest, B_{188} for 3 minutes ineffectively looked for the nest-hole, digging in various places, both within the system and outside it, even as far as 10 m (sic!) from the actual place in which it was situated. It took no more than to replace the blue with black cubes to induce the wasp to alight — after a brief recognition flight ($g = 2 \cdot 2$ sec; i_g — insignificant) — in the proper place and, after a moment, to enter the nest.

Summing up these results, we should state that the variability of the elements of gestalt is tolerated by *Bembex* to an only limited extent.

Now, in turn, let us deal with the problem of b) *the second property of gestalt*: "each configuration may be subject to transposition".

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[8] The result of test 12 is rather surprising. In view of the possibility that *Bembex* does not discriminate qualitatively black and red colours, one might presume that, in this case, B_{136} has displayed a preference to darker landmarks.

The question is to what an extent is the variability of configuration tolerated by Bembex.

During disturbance-*test 15*, after being accustomed to the wreath (32 cm in diameter) consisting of black pine cones, B_{114} did not respond to its conversion into a system of widely scattered cones. She also did not display any confusion when — in her absence — this system was replaced with a triangle, with its side 30 cm long, consisting of black cones.

Fig. 7. Test 16, concerning the second property of gestalt in B_{138}, performed on August 6, 1956. Explained in text

Unfortunately, no appreciable results were yielded by *test 16*, modelled on experiments, described by Tinbergen and Kruyt (1938, p. 332) and van Beusekom, (1948, pp. 205—206). After training B_{138} on a wreath of cones, the latter were distributed in two semicircles. A route of the wasp's recognition flight after its return is depicted in Fig. 7. Despite the fact that the animal was not misted and did not alight in either semicircle, the character of its flight indicated that *Bembex* noticed a certain similarity between these semicircles and the wreath it remembered from the training system.

Test 17 constituted an indubitable evidence of *Bembex's* gestalt perception. After the training on a wreath of 12 alternately disposed discs and hemispheres, B_{44} recognized a "wreath" in three parallel semicircles which were vertically stuck in the ground and formed a triangle (!).

This was confirmed by *test 18* which, for the sake of clarity, let us cite as an excerpt from its record.

Skolimów, July 19, 1960. Sandy, dune-type clearing. Clear, a few cumuli; temperature, 26°C; calm.

> After the removal of a training system, consisting of 12 lacklustre, black hemispheres 4 cm in diameter, disposed in a circle (⌀ 32) around the nest-hole (Fig. 8a),

12^{10} p.m. B_{197} flew away,

To investigate the transposition of gestalt in *Bembex*' perception, I arranged the same elements in the form of a square (Fig. 8b) on the left from the nest.

12^{12} p.m. B_{197} came flying up without a prey, made a recognition flight ($g = 3{\cdot}5$ sec) and alighted on the nest; dug; scared away 3 times, returned and dug again each time.

I scared the wasp away and shifted the system so that it was aligned with the nest;

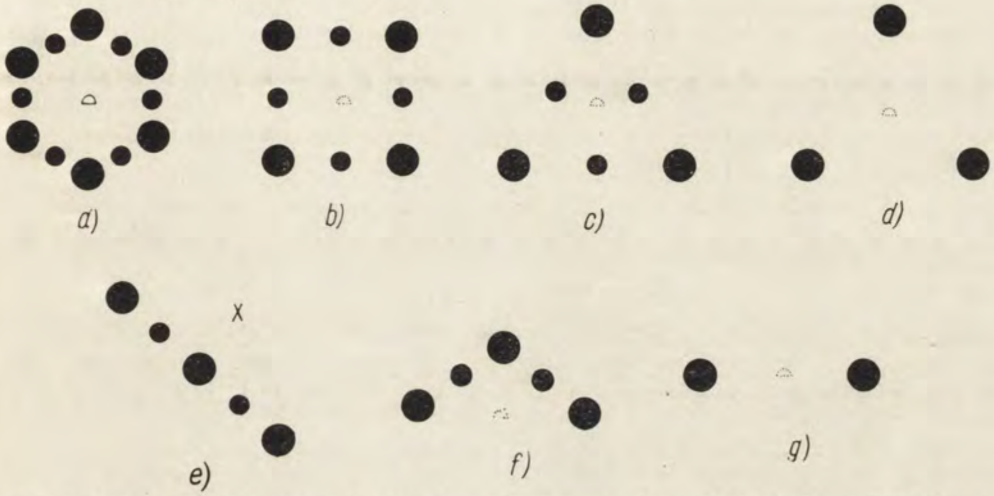

Fig. 8. Training system (*a*) and experimental systems of test 18 with B_{197}, concerning the second property of gestalt, performed on July 19, 1960. Cf. — text

B_{197} returned and, 10 times, preferred the square to the nest.

I changed the system, giving it a triangular shape (Fig. 8c); the wasp tried 2 times to uncover the true nest and, hereafter, 12 times alighted within the triangle consisting of beacons.

Of the entire system, I left only two extreme hemispheres (Fig. 8g); now, B_{197} did not pay attention to the system, took off, flew around the nest, alighted and dug outside the system, 4 times dug in the nest, once more dug outside the system, took off, flew around the hemispheres and

12^{17} p.m. flew away.

I added the third hemisphere which, together with previous two, now formed a triangle (Fig. 8d).

12^{37} p.m. B_{197} arrived without a prey, $g = 5$ sec (significant disturbance), dug within the system, flew around, once more dug, etc. — altogether, 6 times alighted within the system and 6 times — on the true nest (without alighting outside the experimental area).

I scared the wasp away and arranged the blocks in a row (Fig. 8e).

B_{197} flew around, alighted, dug in place x, took off, flew once more, dug in place x, took off, alighted and dug the nest, flew, dug the nest, flew (around the blocks — k) and flew away.

I changed the row into an open triangle (Fig. 8f).

12^{41} p.m. B_{197} arrived without prey but accompanied by a male wasp, both made

> an undulating flight[9], as it is often observed in the common sand wasp *Bembex rostrata* (L.) couples; B_{197} alighted, dug the nest, took off, flew rather chaotically, once more tried to dig in different places.
> I removed the landmarks [...]

A similar experiment was performed on B_{228}. After the training with 6 pine cones, distributed in a wreathlike manner around the nest, new systems were introduced, depicted in Fig. 9 (arrows indicate the places where the wasp tried to dig). Likewise, in a system of 4 pine cones, arranged to form a square, B_{231} recognized the training system which consisted of 6 cones. However, this was not the case of identifying the training with the experimental system because when, after training, B_{228} was offered a choice between the training wreath of pine cones and a square built of these cones, the wasp preferred the wreath to the square with the ratio of 16:3.

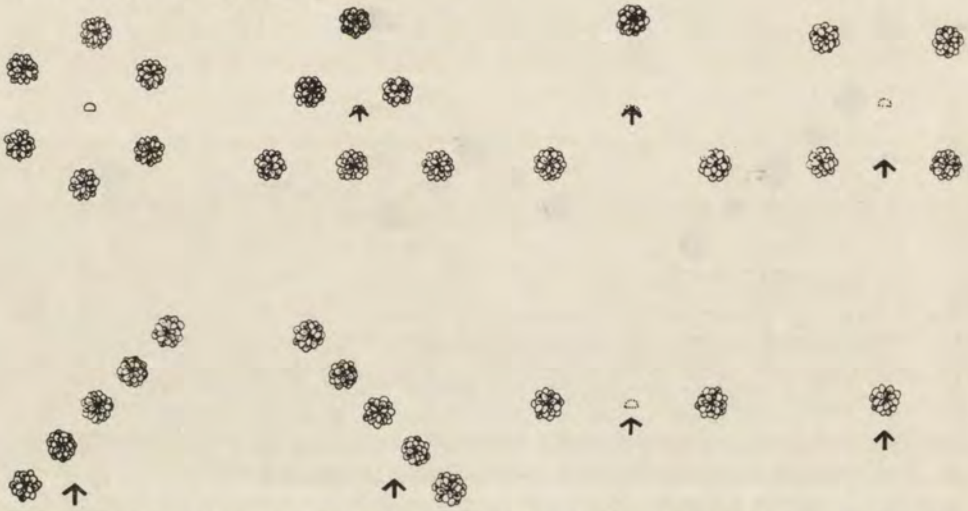

Fig. 9. Training system and experimental systems of test 18 with B_{228} on July 31, 1962. Cf. — text

The capability of female *Bembex* to a complex perception of the configuration of the nest environment landmarks may thus be considered proved (cf. Chmurzyński 1965b). *Bembex rostrata* (L.) tolerates the variability of gestalt to a considerable extent.

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[9] This name is used to determine a translatory motion of the flight, either fast or slow (0·5—1·5 m/sec), having a vertical harmonic component and, therefore, resembling the flight of woodpeckers, chaffinches and wagtails. The line of the flight of this type is marked by characteristically sharp crests of waves. A fast flight involvels as a rule, long waves (about 1 m), whereas a slow one may be either identical in character, or to the contrary, involve short waves (a dozen or so cm) and thus giving impression of a "jumping" flight. In the fligth of the latter type, the wasp's head always faces the fligth direction.

DISCUSSION

Not all the *Hymenoptera* find the vicinity of their nest with an identically great degree of precision. Likewise, not all of them display an identically strong "certainty" of proximate orientation which behaviourally is expressed by a difficulty of disturbing their orientation, i.e. an increase in g or k.

The disturbance-experiments — including those not described in the present paper (cf. Chmurzyński 1960) — convince us of a considerable certainty of proximate orientation in female *Bembex rostrata* (L.). They are in full conformity with data, supplied by previous literature, devoted to this subject. Wellknown are Fabre's (1879 pp. 265—268) experiments on *Bembex* during which this wasp found its way to the nest and alighted in a place in which its entrance was situated despite the fact that it was covered with a stone the size of a human hand or that a layer of a fresh horse manure, or of a moss saturated with ether or of gravel was spread over an area of about 0·25 sq m of the nest-hole environment. Many of Fabre's results were later repeated by Bouvier (1900, 1901) who stated the lack of disturbances in orientation after covering the nest entrance with different objects as, a few small stones, a stone 10 cm in size, a layer of moss, a pile of small twigs or after levelling the sand around the nest entrance and even after piling a small heap of sand on top of the entrance. In the case of *Microbembex monodonta* (Say), a lack of any disorientation was stated by Parker (1917). His tests were carried out after a rain, after changes in the distribution of landmarks, caused by the wind and by his experiments such as, pouring water over the nest-hole environment, covering the entrance with small clods of sand or placing in its neighbourhood pieces of paper, leaves or rubble. Likewise, no response was recorded in *Microbembex* when the nest environment was trampled within a radius of 2 feet. As is known, these results led even to a temporary misinterpretation of the mechanism of proximate orientation in aculeate *Hymenoptera*. Much the same was observed by Molitor (1944) in *Crabro* (*Ceratocolus*) *subterraneus* F. which quickly enough reached nest-hole despite its being covered with a piece of paper 5 sq cm in area or stopped with either a cotton wool wad, or a small stone. Under particularly difficult conditions, a new tunnel close to an obstacle, blocking the entrance was dug by the square-headed wasp. Such relations — as it has already been noticed by Marquenie (1954) are usually found in insects whose proximate orientation is not based on stimuli, coming from the nest itself and, therefore, distinguishing the stage of proximate orientation in these animals we have to depart from the classical criterion of Watson and Lashley (1915); (cf. Chmurzyński 1963, 1964a, b).

The proximate orientation of *Aculeata* which, leaving the nest usually do not stop its entrance, is as a rule less certain. Beetle-wasp, *Cerceris arenaria* (L.) could not find its way when only part of the entrance was covered with paper and leaf-cutter bee, *Megachile sp.* often abandoned its nest after disturbance (Molitor 1933, 1937). Under similar circumstances, a very strong response was also observed in the wasp *Odynerus* (*Ancistrocerus*) *parietinus* (L.) (Molitor 1939). Not all *Apidae* have, however, such a poor certainty of proximate orientation as that displayed by the leaf-cutter bee. Malyshev (1908) proved that *Osmia* Panz. and mining bees (*Halictus* Latr.) deviate from them and, as a matter of fact, they also differ from each other in the character of their response to changes in the environment. It was with a relative tolerance that mining bee responded to changes in the position of its nest entrance, in both the horizontal plane and vertical direction. For all its great precision, much less plastic proved to be the stereometric orientation of *Osmia rufa* (L.). This animal was considerably disoriented when the tube of its nest was drawn out of the ground even a bare 1 cm! This is the price which is paid in a diminished adaptability for an increased specialization.

It resulted from Fabre's (1879, pp. 268—273) works that, in this respect, *Bembex*' plasticity is rather low. Even a partial digging up the entrance part of the nest caused its inability to find the remaining, visible part of the canal and, consequently, a durable disorientation. It was proved, however, by Bouvier's (1901) experiments that a gradual uncovering of its nest-hole by 5—6 cm long sections may be tolerated by *Bembex* provided that each next change is preceded by its getting accustomed to a newly developed situation.

Bee-killer wasp, *Philanthus triangulum* (F.), takes in this respect a midway position. Although, on leaving its nest, it closes the entrance, it is, however, not assigned to digger wasps with a particularly certain spatial orientation. This is manifested by orientation and recognition flights undertaken every time by this wasp, the same as by beetle-wasp. Its orientation is also based on landmarks, closely related with the nest-hole, i.e. a spot of sand, dug out of it, and, in general, different in colour from the entire background (cf. Tinbergen and Kruyt 1938).

Leaving the nest, female *Bembex rostrata* (L.) usually stops its entrance. A nest may be left open only as long as no egg is laid or when the wasp is suddenly scared away. In addition, except the periods during which the soil is very wet and, therefore, hard to dig in, this wasp, closing the nest, digs in its neighbourhood more or less deep holes, sometimes closely resembling the entrance of the true nest and mostly oriented in an opposite direction. These are what may be called "false nest" [10] which form such a characteristic picture that, judging by these landmarks, even an unknown, closed nest of *Bembex* may be discovered by a skilled observer. Perhaps, they play a certain role in the immediate orientation (cf. Chmurzyński 1964a,b).

On the basis of experiments with the use of a complex optical landmark (pine twig), turned around its vertical axis, one arrives at the conclusion that *Bembex rostrata* (L.) mostly — if not always — directs its orientation by terrestrial landmarks and not celestial navigation which is photo (= helio)-menotactic or "oscillo"-menotactic in character. Such a behaviour of *Bembex rostrata* (L.) corresponds to a phenomenon, observed by Baerends (1941) in *Ammophila pubescens* Curt. which, in the case when a small tuft of heath (*Calluna vulgaris*) (L.), situated close to the nest-hole, was moved to a certain distance, dug in the sand not only at an identical distance from this tuft as previously, but also exactly in an identical place in relation to this tuft. A turn of the branch around its vertical axis induced the *Ammophila* to change the direction of its search for the immediate environment of the nest-hole. In such cases, like after a usual parallel shifting of the landmark system within limits of the proximate orientation field, the precision of *Bembex's* orientation in this stage determines the area of the immediate orientation field which, on the average, is about 2·5 cm in diameter. Sometimes, *Bembex* is not, however, inclined to change its position in relation to the points of the compass within an angle of 360° together with turns given to the landmark system. Unfortunately, there are no sufficient grounds for answering the question whether it is the helio- or the "oscillo"-menotactic navigation that is predominating in such a case. This seems, however, improbable (cf. van Iersel and van den Assem 1964, p. 145) and it is more likely that the wasp takes into account more distant landmarks, perhaps even those situated outside the field of proximate orientation (much the same as it probably took place in many cases, cited as an evidence of certainty of proximate orientation in some *Aculeata* which, of course, does not knock the bottom out of the arguments used in those considerations).

To cite van Iersel (1952, p. 392), female *Bembex,* returning to its nest, virtually "chooses the girdles of orientation marks in such a way, that, arriving at one system, it is able to see the following one. The distance between the girdles becomes smaller and smaller, because the wasp must be able to distinguish the more and more detailed landmarks

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[10] Their possible biological character may be partly explained by the facts, I observed several times, of their being dug up by the cuckoo wasp, *Parnopes grandior* Pall., a parasite of the *Bembex rostrata* (L) nests.

of the following system. Arriving at the last girdle before the nest it looks for the landmarks in the proximate neighbourhood of the nest. The bottom characteristics between the systems are of no or only little importance for the wasp. It seems sufficient to learn only some girdles while digging a new nest, leaving out possible marks in between. With a minimum effort the wasp gets the necessary knowledge for finding back its nest". As is known, the landmarks taken into account are primarily optical in character (Bouvier 1900, 1901; Tinbergen 1947, van Beusekom 1948, van Iersel 1952, Chmurzyński 1953, 1964 b) and it is only under special experimental conditions that one may establish the role of smell, hierarchically subordinated to vision (Chmurzyński 1959, 1960, 1964 a). The role of landmarks in orientation depends on their conspicuousness (Chmurzyński 1953, 1957, 1960, 1964a b, 1966). In the present paper, we undertook an attempt to explain how this role is affected by their number and distribution. This problem is to a considerable extent involved in the behaviour of *Bembex* under normal conditions.

As concerns the number and distribution of natural landmarks, we may distinguish the following fundamental types of environments in which there occur the nests of *Bembex rostrata* (L.), insects which — as is well-known — nest on open areas with a fairly loose soil, for instance, sandy clearings of coniferous forests, paths, dunes, etc. (cf. Chmurzyński 1965 a).

The first type of nesting sites includes environments with permanent natural landmarks, occuring in the neighbourhood of the nest, such as grass which provides a sufficient basis for the wasp's orientation in the terrain. These landmarks may be grouped around the nest, sometimes, may be distributed uniformly from the nest outwards and, in other cases, immediate landmarks may be somewhat more distant from the nest which allows one to distinguish appropriate subtypes.

Environments with less abundant landmarks, uniformly distributed over a larger area are assigned to the second type.

Finally, the third type (with two subtypes), opposed to the first, includes such environments in which more distant permanent landmarks are much more abundant than those, occurring near the nest; sometimes, the latter almost do not occur at all.

The inclination, we found in *Bembex,* to prefer the landmarks nearer the nest and to use them for the purposes of proximate orientation, exerts, according to van Iersel's opinion, cited above, a significant influence on the character of this wasp's orientation depending on the environment of its nest. This preference meets no difficulties in the cases of the environments of type 1 and, to a considerable extent, 2. It is well-

-known that in such environments, the training of wasps results in a failure if the terrain has not previously been cleaned of grass (cf. van Iersel 1952, p. 384). Adding new elements, much the same as removing or shifting one or even a few previous ones may evoke at most a poor orientation response. It is only the removal of these landmarks over a fairly extensive area that causes a distinctly visible disturbance, in particular in type 1 environments.

In the case of type 2 environments and even more so of type 3 the inclination of *Bembex*, referred to above, would not guarantee a proper orientation in the environment of the nest. The number of permanent landmarks, occurring in the neighbourhood of the nest is here inferior to that of impermanent ones such as, for instance, hollows in the sand or fallen cones and, therefore, it is easier to change the configuration of these features. Under such conditions, as described by van Iersel (1952, p. 391), the greater the disturbance in the vicinity of the nest, the more intensively the farther environment is used by *Bembeces*. A more elementary tendency to base orientation on a sufficient amount of information, understood as a function of both the number and intensity of landmarks, gets upper hand in this situation. These two interfering tendencies seem to be sufficient for understanding the entire wealth of means of proximate orientation of *Bembex* and, probably, of other *Fossores*. This was given utterance in determining the radius of the field of proximate orientation (R) when, in our formula:

$$R = C - f\left(\frac{L}{D}\right),$$

we submitted the information (Chmurzyński 1963, 1964 a) that — in *Bembex* — it is approaching its maximum specific value ($C \approx 4$ m) when the number and intensity of natural landmarks (L) are at their lowest [the role of disturbances near the nest (D) is decisive for the dynamic character of R]. When, therefore, the landmarks are less abundant, as in environments of type 2, the spatial orientation is based on taking into account memorized cues, found over a more extensive area. The certainty of orientation continues to be considerable which has been observed in the case of B_{81} in test 3 in which it was visible that the stone, in contradistinction to occasional hollows in sand, played the role of one (but not the only) of the beacons. In the environments of this type, new elements added evoke a response only when they are of a sufficiently high orientation significance. It may well be that such were precisely the conditions with which the investigators as, Fabre and Bouvier, had to do. They repeatedly failed to exert an influence on *Bembex*' orientation although, on the other hand, the success of training on conspicuous landmarks cannot be, under such conditions, precluded.

Elements, situated in the proximate orientation field itself, do not close the list of all landmarks playing a certain role in this stage of the return to the nest. Even the orientation and recognition flights, fundamentally related to the field of proximate orientation (Chmurzyński 1964 a) (because of their aim which seems to be to base the orientation on sufficient amount of information), may sometimes — in the case of a very intensive disturbance near the nest — take place outside the range of the proximate orientation field. This happens especially in the environments, assigned to type 3. The orientation of common sand wasps, *Bembex rostrata* (L.) in such environments is most suscepticle to changes, occurring in the neighbourhood of the nest and which may lead even to a complete and durable disorientation. In the case of a terrain where there are conspicuous distant landmarks such terrain is the best for performing training experiments. This is in conformity with the statement of Tinbergen and Kruyt (1938, p. 324) who found that new landmarks are most willingly taken into account by bee-wolf, *Philanthus triangulum* (F.) in an open area. The same applies to honey-bees (Wolf 1927). In the case of scarcity of near landmarks with a simultaneous lack of conspicuous distant beacons, shifting nearer one — and, at the same time, the only — landmark which is situated in the neigbourhood of the nest, does not cause any disturbance (i.e. prolongation of g or k) but the wasp at once starts to dig in a proper relation to this landmark (cf. test 1 with B_{88} and test 3 with B_{81}), which means that in the case of the lack of other reference system, the animal simply "does not notice" any change. Even in such an environment, distant landmarks assist *Bembex's* spatial orientation by determining the field of proximate orientation and the field of immediate orientation does not exceed about 20 sq cm (cf. Chmurzyński 1960). When distant landmarks are more abundant, the orientation is more accurate and more certain. One may presume that these landmarks exert certain influence on the radius of the field of proximate orientation, the same as it is beyond any doubt that the radius of the field of immediate orientation constitutes a function of several variables, in this number, primarily of the abundance, distribution and character of landmarks.

The conclusion on the role of distant beacons in the proximate orientation of *Bembex rostrata* (L.) may be drawn even on the basis of a brief note of Marchand (1900) who describes his experiment rather incidental in character. In the absence of the wasp, he moved the herb *Vincetoxicum officinale* Mnch., situated 50 cm from its nest for a distance of about 60 cm towards an old mill and replaced it with a piece of a broken bottle. Twenty minutes later, *Bembex* alighted directly on the place from which the plant, referred to above has been removed and, disoriented, crawled to and fro, moving its antennae, taking off and alighting again. It took 5 min before — after a brief hesitation — the wasp found its way to the nest. The author's supposition that the plant and the old mill constituted landmarks for this wasp, seems to be quite correct. For our part, we may add another supposition, i.e. that this scene was set in an environment of type 3. An instructive justification of the role of distant cues in the proximate orientation of female *Bembex rostrata* (L.) is met with in experiments, performed by van Iersel and van den Assem (1964).

An explanation of the mechanism of the wasp's tendency to base its orientation on a sufficient number of landmarks may be primarily looked for in a phenomenon which was called by Pavlov an "orientation reflex". This reflex, as an animal's response to perceptive elements new to this animal — and which in our case, occurred when *Bembex* dug its nest-hole — is extinguished only after these elements are organized and, by way of latent learning, given a form of a good gestalt. It is easily imaginable that in addition to a normal award which, in conditioning and forming conditioned reflexes of type 2 (or integrated in the form of trial and error learning — cf. Thorpe 1956) — that may play here a certain role — is represented by finding the nest, a certain role is undoubtedly played by an additional reinforcement, characteristic of an exploratory learning which, according to Thorpe, makes up a component of imprinting, i.e. acquiring an insight. In our case, such an award may be represented precisely by "the fuller organisation of sense data or primary perception into a good gestalt" (Thorpe 1956, pp. 105—106).

A capability to organise visual data into gestalts is known in many insects. It has also been found in female *Bembex rostrata* (L.). In *Bembex*, the assemblage of features in the environment of the nest does not constitute only a certain number of data, independent of each other and which assist each other in their orientation role of beacons, but their set makes an integrated whole as is understood by the concept of gestalt.

Bembex, not less than *Philanthus* (van Beusekom 1948), tolerates the change in configuration when the component elements are kept. A wasp, trained on a closed ring of landmarks, surrounding the nest entrance, recognizes this gestalt as long as the system of cubes or pine cones keeps, to a certain extent, the character of a "closed figure with the nest in its middle". This is manifested by both the wasp's approach to similar systems and small values of i_g and i_k, caused by changes in these systems.

Any doubts, if here we actually have to do with the gestalt perception and not with the training on its components [which might be suggested by the wasp B_{197}'s digging near the "open" row of blocks (Fig. 8e) after a training for the "closed" ring (Fig. 8a)] are dispelled by the fact that *Bembex* is capable of accepting the variability of elements provided that the configuration is kept unchanged. This applies, however, to either the elements similar to each other and hierarchically equivalent as, for instance, red and black cubes, or the elements low-ranking in the hierarchy of visual qualities as flat coloured discs. In such cases, the gestalt predominates over the characters of elements themselves. However, the tolerance of the variability of the gestalt elements is displayed by *Bembex* to a much smaller extent than by honeybee and even by bee-killer wasp, *Philanthus triangulum* (F.) (cf. van Beusekom 1948). It is in particular that *Bembex* directs its orientation by an absolute colour of landmarks to a much greater degree than the latter species; likewise, it is very sensitive to the differences in articulation of these cues.

With regard to the complex of landmarks, it should be stated — and this applies also to gestalt — that *Bembex* uses them in different manner depending not only on their conspicuousness or distance from the nest, but also on their situation in relation to the nest entrance. Of near landmarks, those situated in front of the nest seem to play a greater role in proximate orientation than those disposed behind its entrance.

It seems, however, that *Bembex*' sense of what is situated "in front" and what "behind" is fairly complex. Perhaps, it resembles a sense of the left and right side in small children who, sometimes, are inclined to a "mirrorlike" manner of writing letters or figures, as well as to read many-figure numbers both from the left to the right and vice-versa. A wasp trained on a nest, situated in front of a landmark happens to start its search for the nest behind the landmark (cf. test 2 — digging in *y*). This problem requires, however, special consideration.

The behaviour of B_{220} in test 2 also reveals an inclination to what is called "sidedness", occurring sometimes in these wasps. This problem, well-known to ethologists who study the proximate orientation in digging *Aculeata* has recently been fairly accurately investigated in *Bembex rostrata* (L.) by van Iersel and van den Assem (1964).

SUMMARY

The proximate orientation in female *Bembex rostrata* (Linné) consists in terrestrial landmarks, mostly optical ones. Conflicting tendencies to base the orientation on a sufficient amount of information and on

features, occurring as close to the nest as possible are revealed in this process. Their resultant plays a significant role in determining the extent of the field of the wasp's proximate orientation under definite environmental conditions.

In proximate orientation, in addition to the features of landmarks themselves, a considerable role is also played by their mutual spatial relations as well as those occurring between them and the nest-hole and by their configuration. Near landmarks, situated in front of the nest seem to fulfill more important orientation function than those, disposed behind it.

Although *Bembex*, particularly sensitive to the colour and differences in articulation of landmarks, poorly tolerates any changes in the configuration elements of these landmarks, the organisation of optical cues into gestalts may be considered proved. The variability of gestalt is tolerated by the wasp to a considerable extent.

It is with a great accuracy that distance is estimated by *Bembex* so that, under favourable conditions, it may estimate the situation of the nest entrance with an accuracy amounting to 1·0—1·5 cm.

I would like to express my thanks to Dr. J. Bruner, Miss Ewa Horn, M. A. and Mrs Barbara Lipińska-Skawińska, M. A. for their kind interest and aid in carrying out some experiments.

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Book reviews

Fiziologiia cheloveka i zhivotnykh (Human and animal physiology). Third edition, revised and updated. By S. I. **Galperin** and K. P. **Golysheva.** Edited by M. M. **Nefedova.** Moscow: Izdatelstvo „Vysshaia shkola", 1965, pp. 571, illustrated.

This is a good, straightforward textbook. Its style is simple, clear and direct. It will surely be a great stimulus to an audience at about the level of freshman students taking an introductory course in physiology. It may also prove helpful to an advanced student, physiology teacher and young scholar. Furthermore, it should be welcomed by many readers with general physiological interests.

The value of the book lies primarily in the fact that the subject matter has been given in a substantially condensed form. Yet this condensation has been achieved with little loss of the more essential text. This is of enormous aid to the undergraduate student for whom the brevity and lucidity of an account that brings into one volume the mass of data relating to general physiology are certainly desirable.

The third edition of the Human and Animal Physiology is indicative of the obvious need for this textbook.

There is a number of good points in this volume. The authors attempt to present both sides of controversial questions, and they do remarkably well in discussing the theories that reflect older and modern thinking of research in physiology. One will also find, as the authors point out, where continued work and new knowledge are needed and where one must proceed cautiously. Each chapter contains much historical material and references to outstanding Russian, Soviet and foreign authors. This provides some basis for orientation of the past and present events and discoveries.

The material of the book is discussed from the standpoint of phylo- and ontogeny with emphasis on qualitative and quantitative differences between man and animals. The physiological ideas are treated in the light of dialectical materialism. In general outline the text considers the role of speech and labor in organizing and regulating the development and the various physiological aspects of human organism. It is the authors' aim to indicate that the recognition of the human being as a purely biological creature is inappropriate and likely to prove ineffective, and that numerous physiological phenomena in man cannot be explained in terms of the laws of biology and animal physiology.

The production of the book meets fairly high standards. A comparison of the two first and the third editions reveals significant change in the content. The many first and second edition figures of questionable quality, and by adding a few new pictures. The illustrations, the format, and the fair binding all have resulted in a pretty handsome volume.

Rather than reviewing the entire volume I shall focuse my attention on the topics that were not included in the earlier editions.

Preliminary chapters contain a detailed introduction with the description of the wide variety of topics to be discussed, and the information on the aims and the effectiveness of different physiological methods. Important sections of the book deal with theoretical and practical advances in cybernetics and electronics. They also incorporate information on the modern physiological apparatus. Deserving of particular notice is the stress laid on the computers and electronic machines which are of real value in faciliting the mental and manual efforts of man. At the same time, the writers explain in detail the difference between the electrical and ionic processes in living systems, and point to the importance of the analysis of physiological phenomena for engineering and bionics.

The book contains a large collection of useful information on current achievements in physics, chemistry, and mathematics. This represents an attempt to emphasize the practical application of physiology and related disciplines to medicine, pedagogy and agriculture. A number of notices and biographical sketches of the most outstanding contributors to anatomy, physiology, chemistry and physiology are given.

A survey of the function of particular organs and systems is preceded by a careful description of basic regulatory mechanisms of living organisms.

Chapters concerned with the muscle and nerve physiology offer current views on the anatomy of contracticle and conductive tissues, electrical and humoral transmission, chemistry of nerve activity and muscle contraction, the nature of the muscle and nerve impulse, membrane theory, cell potentials, and the origin of the action potential. They also set forth an information concerning electrical organs. These chapters are followed by a discussion of the origin and evolution of excitation.

From these considerations, attention turns to the central nervous system, synaptic conduction, and newly discovered chemical transmitters. This section of the book emphasizes the diversity of opinion on the basic mechanisms involved in reflex activity. It also offers an adequate description of various forms of central inhibition (presynaptic, postsynaptic, antidromic). Considerable attention is given to the limbic system and reticular formation.

The chapter entitled "The cerebral hemispheres and the higher nervous activity" includes a good deal of new material. Most of the text is organized around recent findings concerning the electrical activity of the cortex in the first years of life in man, when conditioned reflexes are trained and inhibited, and under circumstances of sports and other voluntary muscular efforts. Also the interrelation between the cerebral cortex and reticular formation in the production of biopotentials is debated. There is considerable detail on the recent experimental evidence relating the prefrontal cortex and its affiliated brain structures to higher nervous activity and behavioral inhibition. In addition, this chapter presents a comprehensive and up-to-day summary of ablation and stimulation studies which together provide a basis for understanding the function of individual cortical and subcortical areas. There is consideration of the participation of both the cortex and subcortex in the formation of conditioned reflexes. What one regrets, however, is that this chapter fails to include a great many other studies pertinent to the problem. Curiously enough, *Galperin*, himself an authority on brain localization, gives no evaluation of the work done in his laboratory on the effect of a bilateral premotor cortex lesion on the conditioned diuresis and the motor conditioned reflexes elicited by stimulation of the receptors of the digestive tract.

Arguments are presented to emphasize the role of the basal divisions of the brain in the higher nervous activity. It seems astonishing, however, that the text provides the reader with incomplete information on the *Galperin's* new concept of internal inhibition. Thus, despite a slight mention on page 206, an ultimate understanding of the concept has not been achieved.

One of the noteworthy sections of this chapter discusses in a highly effective way the contribution of labor and speech to the organization of the cortical "representation" areas of kinesthetic and motor functions in man. Much is said about the influence of the hormones and transmitter substances on the higher nervous activity.

The chapter concerned with the physiology of the analyzers (receptor organs) presents an accurate account of recent electrophysiological investigations of sensory functions and goes into much detail on the new findings. It contains a number of new illustrations. There is a detailed analysis of the proprioceptive influence on the viscera (motor-visceral reflexes).

The present volume considers the stereochemical theory of olfaction, and offers information on the volley theory with special reference to the organ of Corti. These theories were not treated in the two earlier editions. Also the new theory of color vision, the present-day views on the sensory code, and a number of other contemporary concepts as applied to sensation are at least mentioned.

One of the most notable changes in the volume is the chapter entitled "Physiology of the motor apparatus", a subject hardly incorporated in any other textbook of physiology known to the reviewer. This chapter primarily deals with the function of the motor apparatus in man, and takes the establishment of habits and physiological principles of motor acts at work, physical exercise and sports for detailed consideration.

In the chapter on the properties of blood also some new material is given. This includes blood coagulation and the role of the nervous system in it, anticoagulants, hemolysis and serologic composition of blood accompanying muscular responses.

The following chapter provides an up-to-date treatment of conduction system of the heart, and gives an interesting account of the changes of the autonomic and humoral regulation of the heart and the vascular system during muscle work.

The chapter on the physiology of respiration contains considerable new information on the regulation of breathing, tissue or internal respiration, and the interrelation between respiratory and circulatory functions.

In the chapter on the functions of the digestive system new techniques in studying the digestive tract, including the isotope tracing technique, are given. The chapter contains also considerable accounts of data on the hormones recently discovered in the digestive tract. Some new material and theory on the absorption from the digestive tract is presented.

The chapter on metabolism gives information on the newly discovered vitamins (for instance, vitamin B_{15} is briefly described). Diets for man and animals recommended recently by the Food and Nutrition Board are given.

The book includes the advances in renal physiology that have been made in last decades. Nervous and humoral control of reabsorption processes is covered in an adequate manner.

Relatively much space is devoted to internal secretion. The authors describe new methods for investigating the internal secretion, newly discovered hormones, vitamins, transmitter substances, and some protein products.

The practice throughout the text is using all measures according to the international system is very fortunate. Such practice as this one is rare indeed.

There are a few defects in the book. Some important questions are compressed into too little space. Certain topics (the current concept of internal inhibition, the motor system in man, and the autonomic nervous system, etc.) are given extremely brief notice. In contrast to the earlier editions of the textbook, the paragraph dealing with speech is skipped altogether. This is a very serious deficiency. Many subjects need more detailed discussion. This can be achieved by substantial enlarging the text of the book in the edition to follow.

In spite of these criticisms, the book constitutes a valuable source of current information on the subject.

N.A. Shustin, Leningrad, USSR

Fiziologicheskie osobennosti detei (*Physiological peculiarities of children*). By S. I. GALPERIN. Edited by N. T. Rybakova and A. M. Pridantseva. Moscow: Izdat. "Prosveshchenie", 1965, 243, illust.

This monograph, concerning the basic features of the physiology of children of school age, was written by Professor Semen Ilich Galperin, an experienced author of textbooks in the field of physiology and psychology. In accordance with a long-standing tradition, the developmental physiology has been an object of lively interest of Russian and Soviet scientists. For this reason the first Soviet textbook, devoted to this important subject, arouses a justified interest. The book in question is mostly based on facts. Fundamental physiological peculiarities of particular systems and organs in children are discussed in 12 chapters. The remaining 6 chapters are more general in character and deal mainly with the problems of periodization of the child's development, as well as with the principles of a proper organization of mental and physical work of children, resulting from physiological peculiarities of the developing organism. The book is illustrated with tables and numerous diagrams.

The small size of this book induced the author to make a rigorous selection of the material. It is only the chapters, devoted to the development of the nervous system and perception which are more extensively treated. This may be, to a certain extent, ascribed to the author's personal interests. Several other systems are discussed almost summarily. The chapter on skeleton may serve as the best example in this respect. It seems, however, that — if only on account of faulty postures so frequently met with in children of school age — the anomalies in the development of skeleton should be much more extensively discussed.

A rich material consisting of many facts is mostly related to the children of school age, whereas earlier development stages have been dealt with rather superficially. Such a selection of the material is justified by the readers for whom this book is mostly intended, that is, students of pedagogical colleges. However, the scarcity of data on earlier development stages, as well as on the mature organism, does not allow the author for a more profound discussion of the data in a comparative aspect, this being to the detriment of this work, devoted to the peculiarities of the developing organism.

Even more than the examination of mature organisms, the studies in the field of the developmental physiology give rise to several theoretical problems such as, influence of environment and adaptive capabilities of a developing organism, nonuniformity of the morphological and functional development of different organs, formation and specialization of different types of reflective reactions of an organism, etc. An emphasis put on these problems, on which Soviet scientists' scope of knowledge is as a matter of fact very extensive, could considerably contribute to the attractivity of this book. It is also noteworthy that, due to the climatic differences and anthropological structure of the U.S.S.R.' population, Soviet investigators are fortunate enough to have an exceptional possibility of comparative studies whose results should — in our opinion — be taken into account, in books of this type.

It is of interest to compare the numerical data, concerning the development of particular functions, which are given in the book in question, with corresponding figures, published in the western pediatric literature. In many cases, differences are observed which, sometimes, are systematic in character. Since, however, the names of investigators or sources of the data cited are given only occasionally, it is difficult to understand what is a true cause of these differences. Is it a method of collecting and elaborating data, or influences of the environment, or anthropological differences? The lack of a list of authors and more important publications in this field make the readers' difficulties in this respect still greater.

Part of my remarks concern the publishers. Some figures are hardly legible and, in my opinion, should be graphically better prepared, much the same as explanations of several diagrams which are rather insufficient.

In addition, a list of errata is absolutely necessary in a book of this type.

The removal of all deficiencies, referred to above, will undoubtedly extend the size of the book which in its present form is primarily a collection of factual data, interesting to those who deal with the problems of the child's physiology.

K. Zieliński, Warsaw, Poland

XXIV International Congress of Physiological Sciences

The XXIV International Congress of Physiological Sciences will be held in Washington, D.C., U.S.A., August 25—30, 1968. The Congress is sponsored by the International Union of Physiological Sciences (IUPS).

Preliminary notices will be mailed in January 1967, and final notices in October 1967. Plans are already being made for special symposia and invited speakers. Specific suggestions for symposium topics or special lectures should be submitted as early as possible to the President of the Congress, Professor Wallace O. Fenn, University of Rochester Medical Center, Rochester, N.Y. 14620, U.S.A.

In selecting topics for symposia it is expected that the Program Committee will give preference to subject of a somewhat controversial nature, but of broad general interest, and not recently covered in an international symposium. For speakers, special consideration should be given to promising young physiologists with active research programs as well as to older men of established reputation.

All inquiries concerning the Congress may be addressed to:

Mrs. Helena B. Lemp
Congress Manager
XXIV International Congress of Physiological Sciences
9650 Rockville Pike
Bethesda, Maryland 20014
U.S.A.

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