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MYELOARCHITECTONICS OF THE POSTERIOR COMMISSURE OF THE DOG'S BRAIN

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(*Received September 1, 1963*)

The purpose of this study was to trace the course of the posterior commissure and to mark out its parts.

To carry out this task, 5 series of sections of the dog's brain were made. These were: 3 series of sections in the frontal, sagittal, and horizontal planes, stained by the Weigert-Wolters method, and, 2 series of sections stained, using alternately Klüver's and Nissl's methods.

Topography of the Posterior Commissure

The posterior commissure of the dog lies on the border of the dorsal portion of the diencephalon and the mesencephalon. It belongs to a complex of commissures, which seemingly form a whole. This complex includes the habenular commissure, posterior commissure, and commissure of the anterior quadrigeminal bodies. It forms a twisted band of varying width in the diencephalon and mesencephalon. In the sagittal section, the band rather resembles the mark of interrogation in shape (Fig. 1).

The proper posterior commissure extends from the base of the habenulae to the anterior prominences of the quadrigeminal bodies. Here, it terminates merging with the commissure of the anterior quadrigeminal bodies without any distinct boundary.

Out of the 3 above-mentioned commissures, the posterior commissure has the largest number of fibres. It is situated in the posterior wall of the third ventricle, just at the entry of the cerebral aqueduct. Above the posterior commissure there is the pineal body, while dorsally and anteriorly it verges on the habenular commissure and the habenulae separated from the commissure by the pineal recess.

The posterior commissure is built in the central grey matter, which joins the grey matter of the wall of the third ventricle orally and passes into the grey matter of the bottom of the fourth ventricle inferiorly.

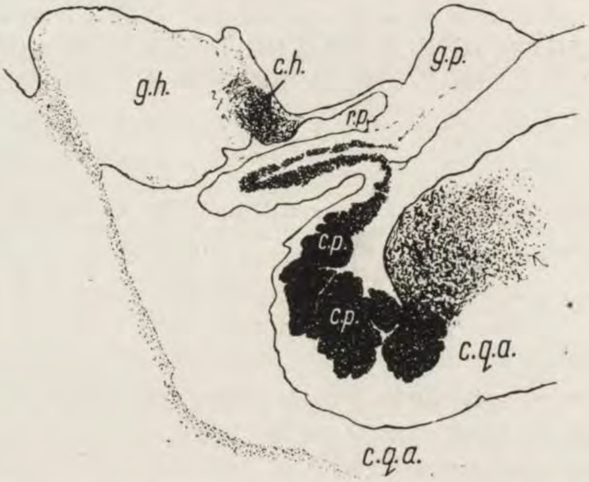

Fig. 1. Sagittal section of the dog's epithalamus. Weigert-Wolters method, semischematic.

The cells of the central grey matter in this region of the brain are grouped in nuclei, of which the most important ones are the nucleus commissurae posterioris, nucleus interstitialis, nucleus of Darkschewitsch, and the nuclei nervi oculomotorii.

The nucleus commissurae posterioris, regarded by most anatomists as common to the fibres of the posterior commissure and those of the medial longitudinal fascicle (Ramon y Cajal 1904, Kappers 1947, Kuhlenbeck 1929), consists of two parts: medial and lateral (Fig. 2). It is situated ventrally to the pretectal and lenticular nuclei and dorsally to the nuclei mentioned above. It extends orocaudally over a distance of about 1150 μ and receives the fibres of the optic tract from the lateral geniculate body (Clara 1959).

The nucleus of Darkschewitsch lies at the entry of the cerebral aqueduct. It is a small group of cells situated ventrally and posteriorly to the nucleus commissurae posterioris. These cells do not differ in shape or size from the mass of grey matter cells surrounding the cerebral aqueduct (Fig. 2a, b). The nucleus interstitialis, the large cells of which

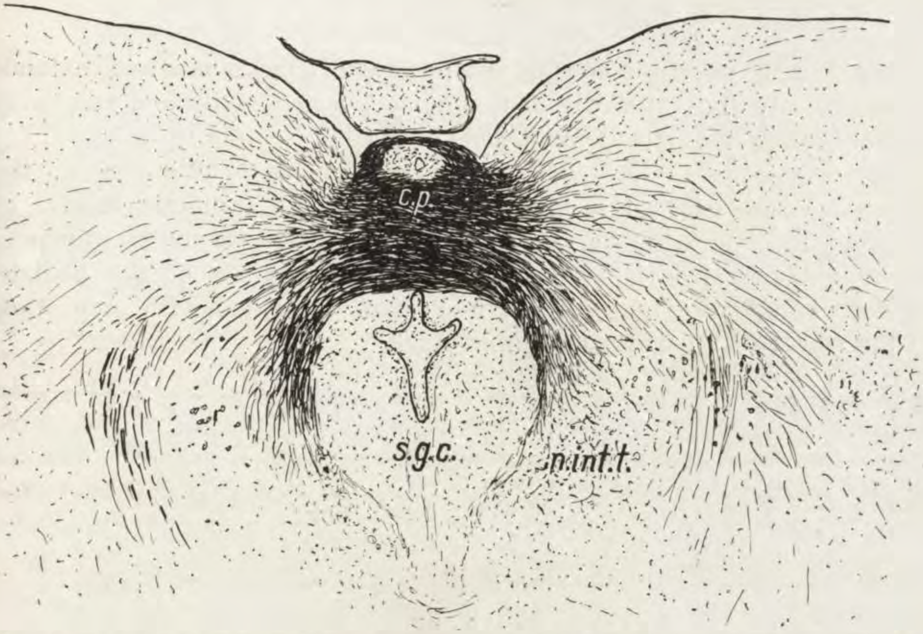

Fig. 2. Frontal section of the anterior part of the epithalamus. Weigert-Wolters method, semischematic.

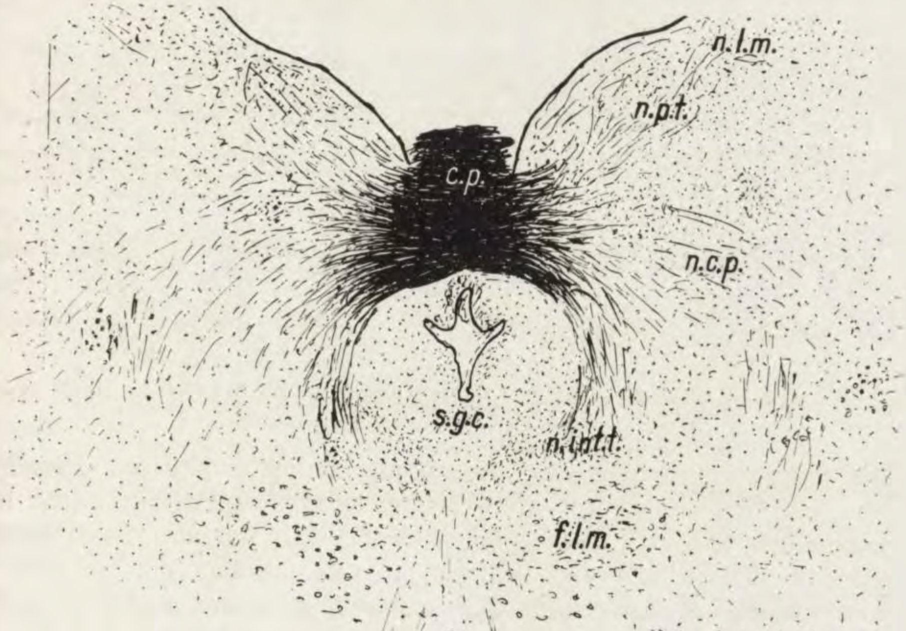

Fig. 3. Frontal section of the epithalamus, about 300 μ from that in Fig. 2. Weigert-Wolters method, semischematic.

border directly upon the cells of the nucleus of Darkschewitsch, extends latero-dorsally and anteriorly to this nucleus and dorsally and anteriorly to the nucleus nervi oculomotorii.

The parasympathetic nucleus nervi oculomotorii autonomicus, the fibres of which reach the ciliary muscle and the sphincter muscle of the pupil, lies under the cerebral aqueduct at a height of the prominences of the anterior quadrigeminal bodies, in the vicinity of the nucleus nervi oculomotorii (Fig. 4). These nuclei are associated with each other by the fibres of the posterior commissure.

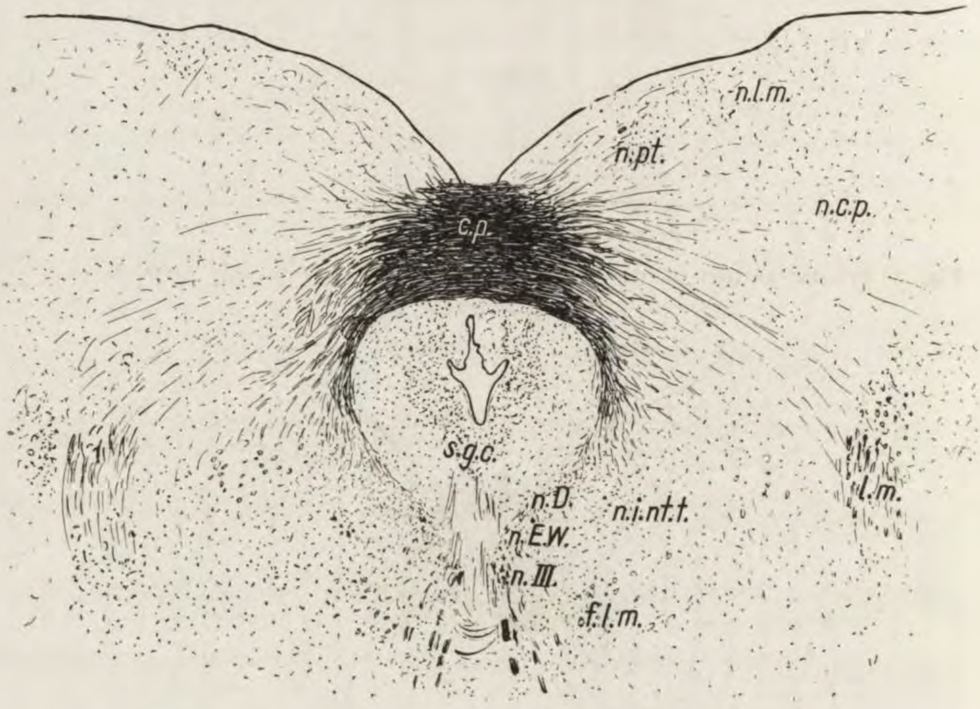

Fig. 4. Frontal section of the epithalamus, about 150 μ from that in Fig 3. Weigert-Wolters method, semischematic.

The nucleus lenticularis of the mesencephalon is situated dorsally to the posterior commissure, while the nucleus preatectalis is found in its neighbourhood but displaced more to the side and anteriorly. Both these nuclei lie medially and ventrally to the pulviner and are considerably pushed out posteriorly as compared with the nuclei already mentioned (Fig. 4). Some fibres of the dorsal portion of the commissure terminate in the region of the nucleus lenticularis of the mesencephalon, and only a few of them pass through this nucleus to the dorsal region of the nucleus praetectalis.

Myeloarchitectonics

The posterior commissure is composed of fibres which originate and terminate mostly among the cells of the grey matter and are grouped in the above-mentioned nuclei or scattered disorderly. The average thickness of these fibres ranges between 1 and 5 μ. In the medial portion of the posterior commissure the fibres reach their maximum thickness, while at its ends they are as thin as 1 μ. The length of commissural fibres is varied. Long fibres with shunts leaving the medial portion of the posterior commissure for more or less remote centres of the mesencephalon and diencephalon predominate. The shorter fibres mingle with them and often have blind ends within the grey matter. In the medial portion, the fibres are very numerous and densely arranged; some of them run through the decussation on to the opposite side and some pass each other parallel without crossing, as in Fig. 3.

In the lateral portion, the fibres scatter in four directions: rostrad, ventrad, caudad, and above all laterad. These last fibres are most numerous, and it is mainly they that form the connection between the centres of both the epithalamus and the metathalamus. All over the commissure are scattered fibres, which are not typical commissural fibres, as they do not connect the same centres of the mesencephalon and diencephalon. They connect various kinds of centres situated on the opposite side.

As far as its shape is concerned, the posterior commissure can be divided into the dorsal, the intermediate, and the ventral part. These parts are best seen in the sagittal section. The double upper band passes, forming a loop, into the intermediate part, from which it is separated by an anonymous recess. Turning in the horizontal plane, the intermediate part, much broader than the upper one, forms the ventral part still broader than the other two. Between the intermediate and ventral parts there is another recess, also unnamed.

In the dorsal part, the fibres are arranged in two fascicles of varying width. The upper fascicle, the fibres of which are directed caudad towards the nucleus lenticularis of the mesencephalon, is about 50 μ wide and borders dorsally upon the pineal recess. The lower fascicle, about 70 μ wide, contains a small number of fibres, which run slantingly caudad to the region of the nucleus lenticularis and mainly downwards, where they are lost among the fibres of the lower part of the posterior commissure. A small number of fibres, which turn to the sides, terminates among the cells of the upper portion of the central grey matter. In this part of the commissure its fibres cross a rather large band of fibres, which emerges from the nucleus habenulae lateralis and tends to the central portion of the mesencephalon (Craigie 1925). The fibres of this band run in the sagittal direction and pass partly above the posterior commissure, interlacing ventrally with its fibres (Fig. 5).

The intermediate part of the posterior commissure is composed of a larger number of fibres than the dorsal. Its thickness increases gradually up to 180 μ. The fibres or fascicles of fibres of this part of the commissure extend mainly horizontally to the sides, and a great part of them terminate in the nucleus commissurae posterioris. Some of the fibres penetrate through this nucleus, join the fibres coming out of its cells, turn downwards and reach the medial geniculate body, where they disappear among the nerve cells of this centre (Figs. 2, 3 and 4).

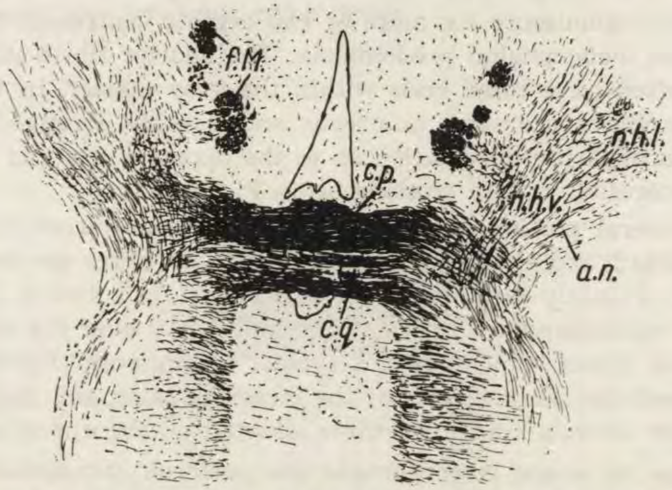

Fig. 5. Horizontal section of the dorsal region of the epithalamus. Weigert-Wolters method, semischematic.

These fibres mark out the lateral boundary of the posterior commissure. In the region of the medial geniculate body some of the fibres of the posterior commissure are crossed by a transverse horizontal band of fibres of the geniculate-tectal tract. The fibres of this tract run to the nucleus of autonomic nerve III in contrast with a majority of fibres of this band, which tend to the anterior quadrigeminal bodies. A few fibres which has passed through the nucleus commissurae posterioris run more vertically downwards and reach the lemniscus medialis, where they disappear among its fibres (Fig. 4).

In the ventral part the thickness of the posterior commissure approximates to 320 μ. Part of the fibres, lying most ventrally reach the nucleus interstitialis and the nucleus of Darkschewitsch, ending just by the entry of the cerebral aqueduct. A small number of fibres penetrate through these nuclei. Some of them, mingling with the axons of the cells of the nucleus interstitialis and the nucleus of Darkschewitsch, are lost among them, and the others run vertically downwards and, forming a gentle arch, reach the nucleus nervi oculomotori. They join its processes and disappear among them.

Many commissural fibres are scattered within the central grey matter surrounding the cerebral aqueduct. In the area of the nucleus interstitialis, nucleus of Darkschewitsch, and nucleus nervi oculomotorii the commissural fascicles pass and cross the fibres of the medial longitudinal fascicle.

SUMMARY

1. The posterior commissure lies on the border of the mesencephalon and the diencephalon. Its appearance in the sagittal section rather resembles the mark of interrogation. It is situated above the cerebral aqueduct, just below the pineal recess. Anteriorly, it butts against the habenular commissure and it borders upon the commissure of the anterior quadrigeminal bodies posteriorly.

2. The posterior commissure can be divided into the dorsal, the intermediate, and the ventral part. The width of the part contiguous to the pineal recess approximates to 50 μ, those of the intermediate part and the ventral part to 180 μ and 320 μ, respectively. The fibres of the dorsal part communicate with the nucleus lenticularis of the diencephalon and the nucleus praetectalis, those of the intermediate part terminate mainly in the nucleus commissurae posterioris, while the fibres of the ventral part reach the nucleus of Darkschewitsch, nucleus interstitialis, the region of the nucleus nervi oculomotorii, the nuclei of the medial geniculate body, and those of the lemniscus medialis.

LIST OF ABBREVIATIONS

an. — fibrae habenulo-tectales
aqu. — aquaeductus cerebri
c.h. — commissura habenularum
c.p. — commissura posterior
c.q.a. — commissura corporum quadrigeminum anteriorum
f.M. — fasciculus retroflexus (Maynert)
f.l.m. — fasciculus longitudinalis medialis
g. h. — ganglion habenulae
g.p. — glandula pinealis
n.III. — nucleus nervi oculomotorii
n.c.p. —nucleus commissurae posterioris
n.D. — nucleus Darkschewitsch
n.EW — nucleus Edinger-Westphal
n.h.l. — nucleus habenularum lateralis
n.h.v. — nucleus habenularum ventralis
n.int.t. — nucleus intersticialis tegmentalis
n.l.m. — nucleus lenticularis mesencephali
n.pt. — nucleus praetectalis
r.p. — recessus pinealis
s.g.c. — substantia grisea centralis

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SOME PROBLEMS CONCERNING THE MECHANISM OF INSTRUMENTAL CONDITIONING*

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I

As is accepted by many students of animal behavior, the course of events in a well established instrumental conditioned reflex is roughly such (Fig. 1): A conditioned stimulus represented either by an external sporadic agent or by an experimental environment (for instance, the Skinner box), after being associated with a definite unconditioned stimulus, starts to produce by way of conditioning a corresponding *drive* (such as hunger, thirst, fear, etc), which from the physiological point of view consists in the excitation of particular structures of the limbic system. This drive, in turn, elicits a definite instrumental conditioned response which had been established to the conditioned stimulus. The response is then followed either by the presentation of food (or any other positive unconditioned stimulus), or by omitting the noxious stimulus. The consummatory reaction in alimentary conditioned reflexes, that is feeding or drinking, or the cessation of the state of fear in defensive conditioned reflexes, temporarily stops the corresponding drive; such an event is indispensable for the formation and preservation of the instrumental reflex.

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In the present paper, I shall not deal with the evidence concerning the last link of this chain indicating that reinforcement does inhibit the drive centre, but I shall concentrate on the statement that excitation of the drive centre intervenes between the conditioned stimulus and the performance of the instrumental act. Here are some of the facts substantiating this view.

First. It is generally known that blocking the drive centre temporarily decreases, or may eventually abolish the instrumental response. And so, if we deal with alimentary reflexes, the more satiated the animal is, the smaller and more delayed is the instrumental response to the conditioned stimulus, until it disappears completely. This also happens when the appetite is lost because of indigestion, a state of fear, etc. Similarly, the calming of the fear centre with chlorpromazine temporarily decreases or abolishes the instrumental defensive response, and so on.

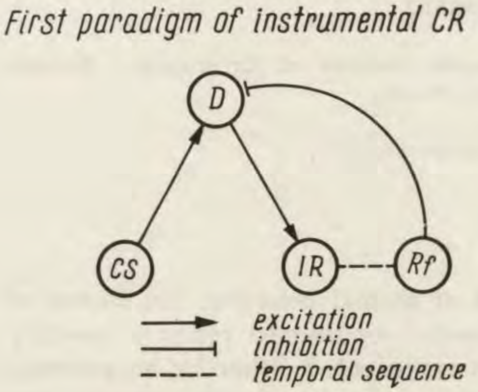

Fig. 1. The simplest scheme of the instrumental conditioned reflex arc. CS, centre of conditioned stimulus; D, drive centre; IR, centre of instrumental response; Rf, reinforcement. Note that CS centre is connected with IR centre by intermediary of D centre. Other explanations in text.

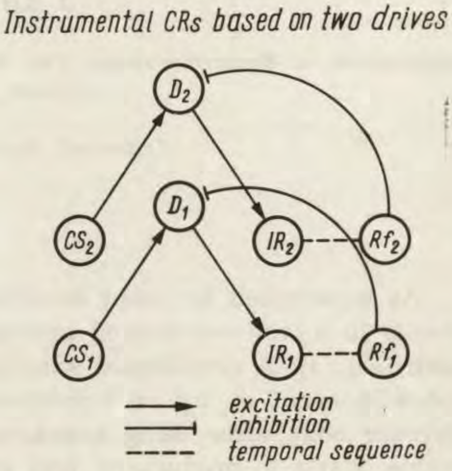

Fig. 2. Instrumental conditioned reflex arcs based on two drives. Connotations as in Fig. 1. Note that both instrumental responses have quite separate reflex arcs.

Secondly. In experiments performed by Wyrwicka, Dobrzecka and Tarnecki (1959) goats were trained using food reinforcement to execute a certain movement, for instance, lifting a foreleg. Electrodes were then implanted into the hypothalamic feeding centre. In the crucial session, the animal was fed before the experiment, and when it totally refused both to perform the trained movement and to eat food presented to it, electrical stimulation of the hypothalamus was given. The goat immediately started to lift the foreleg and did so throughout the period of stimulation, eating voraciously the food offered after each movement.

Thirdly, we have repeatedly shown that in the same experimental situation we can easily train the animal to perform two different motor acts in response to two conditioned stimuli each mediated by a different drive (Fig. 2). For instance, we can teach a dog to lift the right foreleg in response to a buzzer under food reinforcement, and to lift the left foreleg in response to the sound of the metronome by an avoidance procedure, and these two responses are hardly ever interchanged, because they belong to different conditioned reflex arcs. As we shall see later, this does not apply to the situation where two instrumental acts are mediated by one and the same drive, e.g. food.

The next question to be asked is whether the chain of events represented in our paradigm is *sufficient* to account for the occurrence of the instrumental conditioned reflex. The following considerations will lead us to the conclusion that it is not so (cf. Wyrwicka 1952).

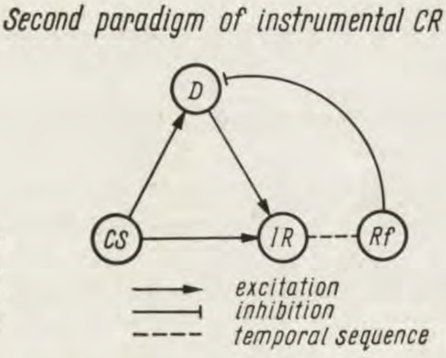

Fig. 3. Improved version of the instrumental conditioned reflex arc. Connotations as in Fig. 1. Note that a new connection linking directly CS centre and IR centre is introduced.

It is easy to see that if the pathway passing through the drive centre were the *only* link connecting the conditioned stimulus with the instrumental response, it follows that an animal subjected to a given drive should always perform *all* instrumental movements which have once led to its satisfaction. But the evidence drawn both from everyday observation, and from experimental data shows that animals may be taught up to a point to *select* different instrumental acts in response to different stimuli under the same drive, depending upon, which of these acts led to its satisfaction in the given situation. This compels us to assume that there exists in our paradigm another association linking directly the conditioned stimulus centre with the instrumental response centre, this association being responsible for the selection of a *proper* response to a particular stimulus. This association is shown in Fig. 3.

Although the two pathways connecting the centre of the conditioned stimulus with the centre of the instrumental response, namely one mediated through the drive centre and the other by-passing this centre, run in parallel, it can be proved that their *joint* operation is indispensable for the elicitation of the instrumental response. In fact, we have already noted in our earlier discussion that when the drive centre is blocked, the presentation of a conditioned stimulus will not elicit the instrumental response, although the pathway CS → IR is intact. On the other hand, we have ample evidence to show that if the animal is brought to a situation totally different from that in which a given instrumental conditioned reflex has been established, it will never perform the corresponding trained movement, even when under a strong drive. For instance, it never happens that dogs fed in the animal house perform there alimentary instrumental movements learnt in the conditioned reflex chamber. This shows that the pathway D → IR alone is also not sufficient for the occurrence of the trained instrumental response.

II

We shall now pass to the next problem, namely that of the mechanism of *inhibition* of an instrumental conditioned reflex when positive reinforcement is withdrawn. Of course, it is well known that if an alimentary conditioned reflex ceases to be reinforced by food, then, after a number of trials, it will be *extinguished*, or else, if another stimulus, similar to the conditioned stimulus, is applied without reinforcement, it will be *differentiated* from the previous one, and will cease to elicit the instrumental response (the so called go-no go procedure).

We shall not go here into a discussion of the much disputed problem concerning the *intimate nature* of such inhibitory conditioned reflexes, this being far beyond the scope of this paper. We shall, however, try to answer the question of, *which* centres are inhibited by inhibitory training, that is, whether inhibition affects directly the centre of the instrumental response through the pathway CS → IR, or whether it affects the drive centre through the pathway CS → D (Fig. 4).

If inhibition occurred along the pathway CS → IR, then, of course, in order to restore the extinguished instrumental reflex one should revert again to its original training, that is to compel the animal to perform the movement in the presence of the conditioned stimulus and to reinforce it by food. If, however, inhibition occurs along the pathway CS → D, then the restoration of the instrumental reflex should be quite different, because, in that case, the mere re-reinforcement of the stimulus should be enough for the reappearance of the learnt movement, since it would unblock the drive centre and thus re-open the pathway leading to the centre of the instrumental response.

The unequivocal answer to this question has been given by Wyrwicka (1952). This author has shown that the mere reinforcement of the conditioned stimulus subjected previously to extinction or differentiation is entirely sufficient for the restoration of the instrumental reflex. This indicates that in that type of inhibitory training the mechanism of inactivation of the conditioned stimulus occurs by inhibiting the *drive centre* and thus blocking the pathway leading through it as shown in graph II of Fig. 4.

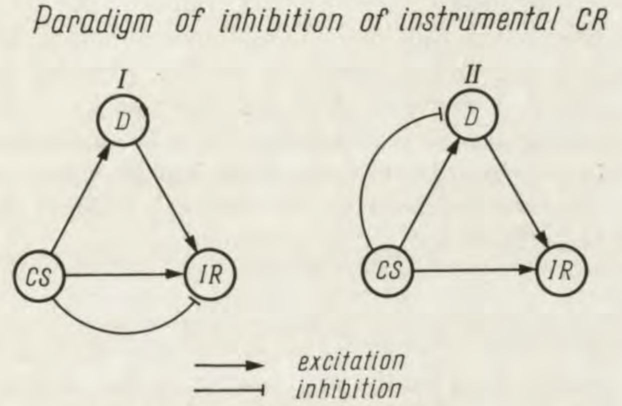

Fig. 4. Two possible schemes of inhibitory instrumental conditioned reflexes.

Connotations as in Fig. 1. Note that in graph I inhibitory connection is directly formed between CS and IR; in graph II, inhibitory connection is formed between CS and D. Other explanations in text.

There are other facts fully corroborating this conclusion. As was shown long ago by Miller and myself, if in the process of extinction or go-no go differentiation we record both the instrumental response and the salivary response to a conditioned stimulus, we observed that their decrease and eventual disappearance occurred at much the same time (Konorski and Miller 1936). This fact again suggests that the disappearance of the instrumental response is closely related to the inhibition of the feeding centre. Another fact, even more impressive, is that when, after a prolonged non-reinforcement of a given stimulus, the food is again offered, the animal often refuses to take it for a few seconds, or even longer. This is again a visible sign of the strong inhibition of the feeding centre produced by the inhibitory stimulus.

And so, extinction of the instrumental reflex, or its differentiation by the go-no go procedure, occurs in exactly the same way as extinction or differentiation of the classical conditioned reflexes, namely by inhibiting the drive centre, and not, more directly, the centre of the instrumental response.

It may be added that quite a different situation takes place when the instrumental response to the given conditioned stimulus is abolished not simply by non-reinforcement of that stimulus, but by its reinforcement in the case when the instrumental movement is *not* performed. In this case, the alimentary response to this stimulus together with salivation is totally preserved, while inhibition of the instrumental response occurs along the direct pathway CS → IR, according to graph I of Fig. 4. Therefore, in order to restore the instrumental response to the stimulus we must return here to the original training and teach the animal anew to perform the given movement.

III

We have spoken so far on the organization of the simple instrumental reflex and its extinction or differentiation through the so called go-no go procedure. Now we shall pass to another type of experiment in which we teach the animals to perform two different movements each in response to a different stimulus but under one and the same reinforcement. We may recall that this task is quite an easy one and does not require any special differential training if both movements are mediated by two different drives (e. g., food and fear). However, the situation is much more complicated, when only one drive is in operation, and the animal has to select the proper response only on the basis of cues provided by the appropriate conditioned stimuli, as is schematically represented in Fig. 5.

These experiments were performed by Ławicka (1963) who applied a simple double choice technique, in which one stimulus signalled a locomotor response to the left foodtray and the other one signalled a locomotor response to the right foodtray. Two tones of different pitch sounding from the same loudspeaker were used. We thought that such a task would be extremely easy for dogs, who, as is well known from earlier Pavlovian times, are great experts in tone discrimination and can solve the go-no go differentiation very promptly, even with quite a small difference in tones. However, to our great amazement, the task of go left-go right differentiation to two tone frequencies appeared to be almost insolvable, unless the difference between them was greatly increased.

However, if two *identical* tones were given from *two different places*, for instance, one sounding from the floor, and the other one from above, the go left-go right differentiation was promptly established. But if these tones were applied in go-no go differentiation, the task appeared to be, on the contrary, very difficult, and when the angular distance between them was relatively small, there was no sign that the dogs were able to cope with the task at all.

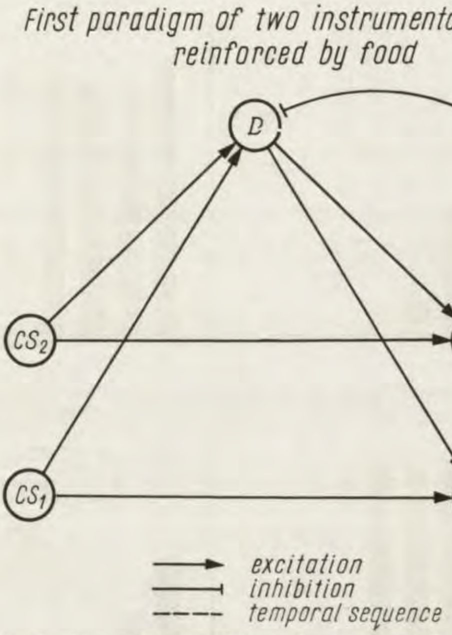

Fig. 5. The scheme of two instrumental conditioned reflex arcs based on the same reinforcement.
Connotations as in Fig. 1. Note that each CS centre is connected directly with its proper IR centre, but it is connected through the D centre with both IR centres.

The results from all these experiments are represented in Fig. 6. Each graph is the mean of data obtained from several dogs.

The upper graph on the left represents the tone frequency differentiation in the go-no go procedure taken from Brutkowski and Dąbrowska's experiments (1963). The positive tone was 1000 cps, the negative one was 700 cps. The intertrial intervals were 1 min. In spite of this rather small difference between the tones, training occurred rapidly and already in the third 90-trial block the criterion was reached. However, when in Ławicka's experiments two tones much more remote from each other (300 cps versus 900 cps) were used in go left-go right differentiation (with the same intertrial intervals), the task seemed to be unsolvable for the dogs, since after four 90-trial blocks (that is after

360 trials) no progress was made (upper right graph of Fig. 6). Only when in further training the difference between the tones was increased by replacing the tone of 900 cps by 1500 cps did the performance of the animals improve. But it was noticed that this improvement was due to the fact that to the high tone the animals developed a strong orienting reaction consisting of a slight startling and pricking the ears. If for some reason this response failed to appear, or, on the contrary, it did appear to the low tone, the animal was sure to commit an error and go to the wrong foodtray.

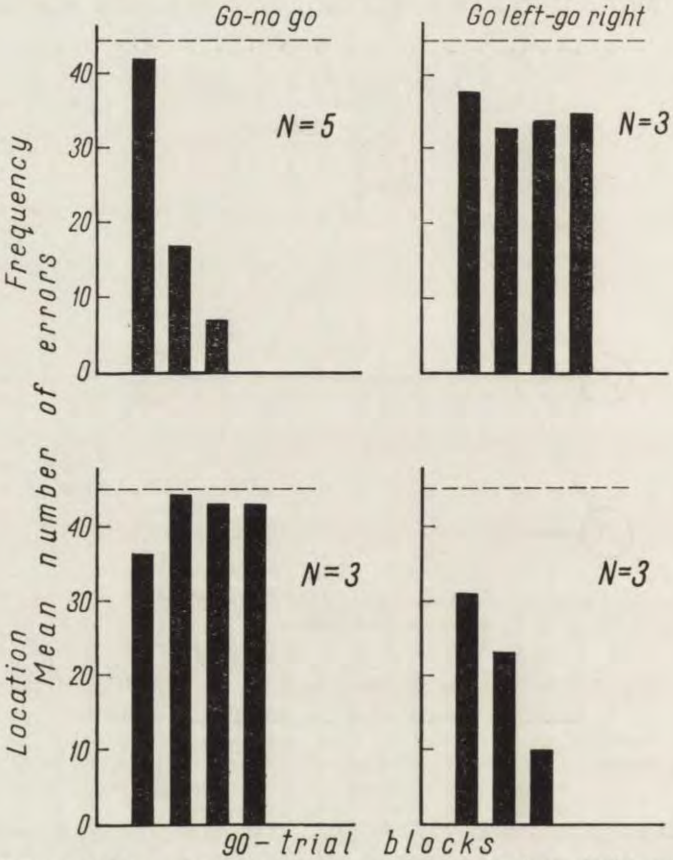

Fig. 6. Differentiation training according to four different experimental procedures.

Each column denotes the number of errors in 90 trials being the average of data obtained from several dogs (N). Broken lines denote the chance level of errors. Note that tone-frequency differentiation in go-no go procedure and tone-location differentiation in go left-go right procedure are easy for the animals, while tone-frequency differentiation in go left-go right procedure and tone-location differentiation in go-no go procedure are very difficult. Other explanations in text.

The lower graphs of Fig. 6 represent the tone location differentiation, one and the same tone sounding from two loudspeakers, one situated on the floor, and the other one hanging 6 feet above the floor. It is seen on the left graph that in the go-no go procedure there was no progress in the training even after four 90-trial blocks. On the other hand, when the same stimuli were used in the go left-go right procedure, the animals reached criterion in the third block, that is after 180 trials.

In order to show how much the dog is directed by the different places of the sounds with total disregard of their quality in the go left-go right differentiation we shall briefly describe another experiment performed by Ławicka at a time when the above relationship had not yet been discovered.

The dog was taught to go to the left foodtray in response to the buzzer and to the right one in response to the metronome. Both stimuli were situated at the starting platform, but since the table there was too small, only the buzzer was located on it while the metronome was put on the floor. In one experimental session, the metronome was put on the table and the buzzer on the floor. The dog ran now without any hesitation to the left foodtray in response to the metronome and to the right in response to the buzzer. And so, while the *experimenter* has learnt that the metronome meant presenting the bowl in the right foodtray and the buzzer in the left foodtray, with total disregard of where the apparatuses were situated, for the dog only the position of the apparatuses mattered and not the sounds produced by them.

In view of the significance of these findings it seemed important to verify them by our usual methods, that is, with the dog placed on a stand in the sound-proof chamber and using the lifting of the leg as an instrumental response. These experiments have just been performed by Dobrzecka and myself.

First, we tried to teach the dog under food reinforcement to lift his right foreleg in response to the metronome and his left foreleg in response to the buzzer, both stimuli being situated one near the other in front of the animal. This proved to be unsuccessful and the animal developed a heavy neurosis becoming unfit for further experimentation. In a different dog, the procedure was similar, except that the stimuli were located in *different* places, the buzzer being placed behind the stand and the metronome in front of it. In this case the differentiation was established and the animal learnt to perform the movement of the right foreleg in response to the metronome, and of the left foreleg in response to the buzzer. It was observed that the lifting of the right foreleg was always preceded by the animal looking forward toward the place of the metronome, and the lifting of the left foreleg was preceded by a backward orienting reaction in the direction of the buzzer.

Now again the crucial experiment was performed in which the places of the stimuli were interchanged: the metronome was located behind the dog and the buzzer in front of him. The responses of the animal were quite unequivocal: to the metronome he displayed now a backward orienting reaction followed by the movement of the left foreleg, while in response to the buzzer he looked forward and lifted his right foreleg.

IV

The present results force us to discard a long held view on the mechanism of differentiation, or discrimination, as the procedure is usually called in American literature. Most psychologists have been accustomed to think that any differentiation, be it the go-no go procedure or the go left-go right procedure, simply reflects the *perceptual capacity* of the animal and what the subject does learn is merely to *discriminate* between the two cues presented to him. Once the cues are discriminated the task was thought to be solved and this or that experimental procedure was supposed to serve merely as a tool to reveal this very fact. Only some students, under the influence of Pavlov's ideas have been ready to admit also the role of inhibition of unreinforced responses as a factor determining the course of differentiation training.

Taking into account our present results we see that there is still another factor, hitherto not suspected at all, which influences to a large extent the course of differentiation. It is that the animal uses quite different cues when he is confronted with go-no go differentiation from those he utilizes when confronted with go left-go right, or, for that matter, lifting the left leg-lifting the right leg differentiation. In the first procedure, he principally utilizes the differences in the qualities of both stimuli, while in the second case the decisive role is shifted to the difference in the *orienting reaction elicited by each stimulus*. This is why the tone frequency differentiation is easy for a dog in the go-no go procedure but not in the go left-go right procedure, while with tone location differentiation the opposite is true.

These facts which seem to be rather puzzling for our present concepts yield themselves to a natural explanation by means of our schemes.

For this purpose it is sufficient to slightly modify our last paradigm by supplementing the direct pathway CS → IR by an additional link consisting of an orienting reaction to the conditioned stimulus and the proprioceptive stimulus generated by it. As seen from this modified paradigm (Fig. 7), the pathways connecting both conditioned stimuli with the drive centre start directly from the CS centres. Since as stated earlier, the go-no go differentiation, just as food-fear differentiation, is based on these very pathways, it is clear that in *this* differentiation the quality of the conditioned stimulus plays a decisive role. On the other hand, the go left-go right differentiation is based on the pathways linking the conditioned stimuli directly with respective instrumental responses, and therefore, according to the new version of our paradigm, in *that* differentiation the decisive role is played by orienting reactions elicited by these stimuli.

A possible misunderstanding which needs to be explained concerns the so called *simultaneous* discrimination of visual stimuli by the go left-go right procedure. It is well known from numerous experiments performed on cats and monkeys that when two food wells are marked by two different figures, or objects, only one of them signalling the well filled with food, the animals easily learn to approach the correct cue. Thus in this case the go left, or go right response is totally determined by the visual cue with no intervention of any proprioceptive stimulus.

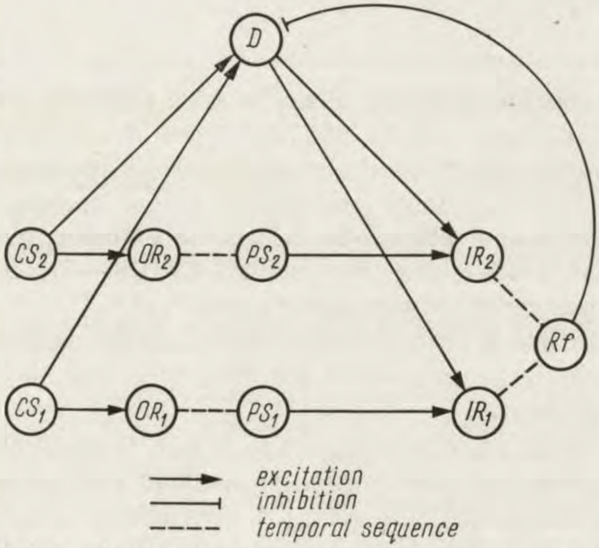

Fig. 7. The improved version of the scheme of two instrumental conditioned reflex arcs based on the same reinforcement.

OR$_1$ and OR$_2$, centres of orienting responses to CS$_1$ and CS$_2$ respectively. PS$_1$ and PS$_2$, centres of proprioceptive stimuli generated by these responses. Other connotations as in Fig. 1. Other explanations in text.

The essential difference between this procedure and that described above seems to be obvious. Since approaching one of the figures leads to food and approaching the other one does not, the animal gradually learns to display a positive response towards the first figure and to inhibit the response to the second figure. Thus, as a matter of fact, we are dealing here with the go-no go differentiation, which, as pointed out above, may be totally determined by exteroceptive stimuli. The only difference between this procedure and the classical Pavlovian go-no go procedure is that in the latter there are separate go- and no go-trials, while in the procedure now under discussion both a go-response and a no go-response are squeezed, so to speak, in a single trial. As is well known it is easy to separate these two responses simply by presenting in a single trial only a positive figure, or only a negative figure, a procedure identical to the Pavlovian differentiation.

V

The major conclusion which seems to arise from the work described here is this. It appears that in different types of conditioning different aspects of stimuli are preferentially picked out by the animal as guiding clues: in classical conditioning, represented in our paradigm by CS → D connections, the animal prefers to utilize the exteroceptive cues, while in instrumental conditioning, represented by CS → IR connections, it makes use primarily of proprioceptive cues.

Now the important problem arises, namely what is the scope of applicability of this principle, which we propose to call the cue specifity principle in learning.

As far as classical conditioning is concerned, there is plenty of evidence to show that not only exteroceptive but also interoceptive and proprioceptive stimuli may be used for the differentiation training, although it is almost certain that exteroceptive stimuli are the most adequate. However, the situation is much less clear in respect to the instrumental conditioning.

First, we do not know whether the proprioceptive link intervening between the exteroceptive stimulus and the response is really indispensable for all modalities of stimuli and all types of instrumental responses. In experiments with Dobrzecka (1962), we have recently shown that when tactile stimuli applied to the distal parts of the limbs are used as conditioned stimuli, it is very easy to teach the dogs, under food reinforcement, to lift selectively that leg to which the touch is being applied. It seems that here the cues determining the instrumental response are provided by the tactile stimuli themselves, and we have now some evidence that the anatomical connections between the sensory and the motor cortex contribute to the specifity of the given response (Konorski and Dobrzecka 1962). And so, the principle stated above has some restrictions even for dog.

Secondly, the problem arises as to whether this principle is also valid in respect to other species, especially those situated higher in the phylogenetic scale. There is no doubt that in man different motor responses can be easily established to different auditory signals, and here the intervention of the orienting reaction for selecting the proper motor act seems to be superfluous. But whether the same is true for monkeys we do not know.

It seems that the present findings can be understood on the basis of a hypothesis put forward several years ago by Konorski (1948). According to it, "actual" (i.e., functional) conditioned connections between two centres can be established only when these centres have been already linked by "potential" connections represented by the corresponding pathways developed in ontogeny.

As far as classical conditioned reflexes are concerned we have plenty of evidence to show that they may be formed to virtually any modality of stimuli, either extero- or proprio- or even intero-ceptive. This indicates that the limbic system representing the higher order centres of unconditioned reflexes is linked with every analyzer by potential connections, which can be transformed into actual connections by the appropriate training. We do not go now into the problem whether corresponding pathways run directly from the particular analyzers to the limbic system, or whether they simply connect the analyzer of the conditioned stimulus with that of the unconditioned stimulus. Since the biological role of classical conditioning is that of "signalling" the unconditioned events by neutral stimuli which happen to procede these events (cf. Pavlov 1927), the appropriate central organization accounting for this function seems to be obvious.

Quite different, however, is the situation in respect to instrumental conditioned reflexes. As seen from the present results, we have good evidence to believe that the auditory analyzer (and perhaps other extero-ceptive analyzers, too) is not potentially connected with centres responsible for instrumental responses. Only the proprioceptive stimuli generated by other movements, and tactile stimuli administered to the limb taking part in the motor act, may be utillized by the dog as agents determining the instrumental response. In other words, the connections involved in instrumental conditioning lead only (or in most part) from the centres of the proprioceptive analyzer to the centres of motor responses.

Since the present experiments are only the first steps along this line of investigation, further experimental work is needed to elucidate in detail the functional architectonics of the higher nervous centres involved in classical and instrumental conditioning.

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THE EFFECT OF PRETRAINING ON THE ACQUISITION AND EXTINCTION OF AVOIDANCE REFLEX

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Exceptional stability of the avoidance conditioned reflex (CR) after relatively short training is well known (cf. Konorski and Miller 1933, and Hilgard and Marquis 1940, Schoenfeld 1950, etc.). However, there is a wide variability in the rate of acquisition and in the stability of the avoidance reflex among animals of the same species even when exactly the same methods are used. In Solomon and Wynne's experiments (1953), the length of training to criterion measured by the total duration of electrical shock applied as negative reinforcement varied in different animals as much as from 10.1 sec. to 454.9 sec. It then may be concluded that while, in most animals, the criterion was reached after a short training, in some of them, the electrical shock had to be applied for a very long period of time (escaping instead of avoidance).

In experiments performed on dogs of different breeds, James (1953) found quick acquisition of the avoidance CR in active dogs with strong defensive reactions, whereas in the hound type of dog with relatively weak emotional reactions, the avoidance CR was not stable even after a long training. The relation between the emotionality and rate of development of avoidance CR is even more intimate: according to the results obtained by Mowrer and Lamoreaux (1942), Mowrer (1947, 1951), Solomon and Wynne (1953), Wynne and Solomon (1955), Kamin (1954), Brush, Brush and Solomon (1955) and others, the emotional reaction to the conditioned stimulus (CS) appeared immediately before the first avoidance response. One can suppose that any factor which changes the speed of establishment of the strong conditioned fear responses to the CS will also change the speed of acquisition of the avoidance CR (Wynne and Solomon 1955). Among such factors, the differences in experimental procedure are of especial interest because they enable us to establish a fear CR to CS before or after any instrumental training.

The aim of this paper is to test the influence of some experimental procedures on the rate of acquisition and on the stability of the avoidance CR.

MATERIAL AND METHODS

20 adult male cats were used. Experiments were carried out in a cage, 65 cm. × 55 cm. × 40 cm., with a floor-grid to apply electric shock to the paws of the animal. In the middle of an oblong wall of the cage, 10 cm, above the floor, a bar, 10 cm. × 2 cm, was located. The bar could be removed through a slit in the wall. Its automatic return was secured by means of a spring. The cage was placed in a sound-proof CR-chamber.

The CS was a mild tone of about 60 db., and 2000 c.p.s., applied through a loud-speaker from a tone-generator. Alternating current of 50 c.p.s. and about 20 to 30 volts from a transformer was used as the unconditioned stimulus (US). Avoidance (and/or escape) response was the bar-pressing reaction, which automatically and immediately terminated the CS and/or the US. When the avoidant movement did not appear during 5 sec. of the CS, the US was switched on and both stimuli were on until the animal responded.

Each experimental session consisted of 10 trials, the intertrial intervals lasting about 1 min. Each trial was recorded on a kimograph, speed of tape 0.5 cm. per sec. The latencies of the bar-pressing responses were calculated from the records.

Some cats remained sitting with the paw still on the bar after the trial was terminated. In these cases, the bar was removed for a while and put back when the animal took its paw away from the slit.

The animals were divided into four groups.

Group 2. The experiments began with conditioning a fear CR to the CS. The very beginning of testing: the CS was given for 5 sec., and when the avoidant movement did not appear, the US was added and both stimuli were switched off only when the bar was pressed.

To make the acquisition of bar pressing easier, in the beginning of training, a platform, 25 cm. × 25 cm., was used as a prolongation of the bar. Then this platform was changed to a smaller one (25 cm. × 12 cm. and, subsequently, 12 cm × 7 cm.). After 10 to 20 trials, the bar-pressing response was established, and no platform was then necessary.

Group 2. The experiments began with conditioning a fear CR to the CS. The classical defensive conditioning procedure was used: each trial started with the CS, and 5 sec. later the US was added for another 0.5 to 1.0 sec. regardless of what the animal was doing. The bar was present in the cage, but accidental pressing of the bar (which happened very rarely) did not terminate the CS. After 30 trials (3 experimental sessions) of such pretraining the procedure, which had been used in Group 1, was introduced to train the avoidance reflex.

Group 3. In this group, no CS was applied in the beginning of experiments and the animals were first taught to escape from shock by the same procedure as in Group 1. After three days (10 trials daily) of such escape pretraining, the regular avoidance procedure was introduced.

Group 4. First, the escape instrumental response was established in exactly the same way as in Group 3. Then, the classical conditioning procedure which was identical with that of Group 2 was used for another three days. After such double pretraining, experiments were run according to the regular avoidance procedure.

Except for the beginning of training, each experimental group was treated identically. The avoidance conditioning training was carried out until the criterion of 90 correct responses in 100 consecutive trials was reached. By the *criterion number* we mean the number of trials from the moment when regular avoidance procedure was applied and excluding 100 trials during which the 90 per cent level was reached; the latter trials are termed *criterion trials*.

After reaching the criterion, the avoidance CR was extinguished during 10 sessions (10 trials daily). The method consisted in delaying the termination of the CS beyond the moment of performance of the avoidant movement (Fonberg 1952, 1960, Bregadze 1953, Bregadze and Akhmeteli 1953). In these experiments, the CS lasted 5 sec. independently of how the animal behaved and no US was used. After 10 experimental days, the same procedure as before extinction was applied and the avoidance CR was quickly retrained.

RESULTS

1. Behavioral changes in avoidance conditioning

Group 2 (*classical conditioning pretraining*). After several pairings of the CS with shock, the animals of this group showed general excitation and a clear defensive response to the CS manifested by mewing, piloerection, urination, defecation, attempts to escape from the box and, occasionally, panting. Sometimes, the cats when hearing the sound of the tone hid in a corner of the box. When the pretraining had been completed and the training of the terminating movement had begun, most of the cats displayed a violent general motor activity, and all of them, very quickly learnt to jump on the platform, and, after a few sessions, to press the bar. The first avoidance reactions appeared during the first day of the instrumental training and the consolidation of the avoidance response was rapid. The bar-pressing response usually had a tonic character, the leg remaining on the bar after the end of the trial. In the beginning of experiments, intertrial responses were observed, but, in the course of training, they gradually disappeared, and tonic terminating movements changed into phasic ones. These changes of behavior indicated a gradual weakening of the general defensive reaction during acquisition and consolidation of the avoidance reflex.

Group 3 (escape pretraining). The shaping of the bar-pressing response was in this group also very rapid. In the beginning of the pretraining, the US evoked a strong general defensive reaction, but when the latent period of the escape response shortened, the animals became quiet.

When the CS was introduced, it evoked only a slight orienting reaction, whereas, a manifest defensive reaction to the CS was absent for many trials. During the period of acquisition of the avoidance CR, as well as during the criterion trials, the cats of this group were much calmer than those of Group 2. The intertrial responses appeared only occasionally, and the terminating movement had, as a rule, a phasic form: after pressing the bar, the cats removed the leg from the bar without withdrawing it. The acquisition of the avoidance CR took much longer than that in Group 2.

Group 4 (escape followed by the classical pretraining). The shaping of the bar-pressing movement was exactly the same as in Group 3. During the next three days of classical conditioning, the behavior of animals of this group was almost the same as in Group 2 although a strong fear response developed a little later.

In spite of the fact that both the bar-pressing response to the shock and the fear response to the tone were established before the avoidance procedure started, the avoidance training was no shorter than in Group 3. Although some cats of this group showed strong fear CR to the CS, even from the very beginning of avoidance training, the avoidance CR was irregular over a long time.

Group 1 (without pretraining). All animals of this group were treated identically from the very beginning of training. However, it appeared very soon that this group was not homogeneous. Some cats showed a strong general defensive reaction to the CS and they developed the avoidance CR as rapidly as those in Group 2. The bar-pressing response in these cats (subgroup 1a) had also a tonic character and intertrial responses were observed. The remaining cats (subgroup 1b) behaved exactly as those in Group 3, with a weak fear CR to the CS, slow consolidation of the avoidance reflex and a phasic form of the terminating movement.

2. The rate of acquisition of avoidance CR

As seen in the Table I, all experimental animals can be divided into two quite separate categories. Cats of Groups 1a and 2 belong to the first category. Acquisition of the avoidance CR is very rapid and does not exceed 45 trials. The second category comprises Group 1b, 3 and 4.

The cats of this category learnt very slowly, the criterion number being not less than 77 trials.

The results obtained were examined statistically by the method proposed for comparison of two sample means, unpaired observations and unequal variables (cf. Steel and Torrie, 1960 p. 81), using the square root transformation of the raw data. It was found that the difference of Group 1a versus Group 3 is significant at the level $p < 0.01$, the differences Group 1a versus Group 1b, Group 1b versus Group 2 and Group 2 versus Group 3, at the level $p < 0.02$, and difference Group 2 versus Group 4 at the level $p < 0.05$, all other differences between groups being not significant statistically. Thus, the small differences in rates of acquisition of avoidance reflex between groups belonging to the same category are not significant, whereas nearly all differences between groups from different categories are significant. It is necessary to mention that, when the Group 1 as a whole is concerned, the differences between this group and the others are statistically not significant.

Table I

The rate of acquisition of the avoidance reflex

Group	Pretraining	Number of animals	Criterion number	
			Mean	Range
1	no pretraining	7	104.7	35—188
1a	„	*3*	*41.7*	*35—45*
1b	„	*4*	*152.0*	*129—188*
2	classical	4	19.0	6—38
3	escape	4	119.0	103—134
4	escape-classical	5	147.2	77—217

Table II

The mean number of avoidance and escape responses during acquisition and stabilization of avoidance reflex

Group	Pretraining	Total number of trials	Number of avoidance CR	Number of escape CR
1	no pretraining	208.6	131.8	76.8
1a	„	*146.7*	*109.0*	*37.7*
1b	„	*255.0*	*148.8*	*106.2*
2	classical	122.5(152.5)	97.0	25.5
3	escape	220.0(250.0)	151.7	68.3(98.3)
4	escape-classical	248.0(308.0)	179.2	68.8(98.8)

In brackets there are the corrected numbers of trials and escape responses when the pretraining trials are included.

Note that if the pretraining trials are counted for Groups 2 and 3, the data for Groups 1a and 2 and for Groups 1b and 3 are nearly the same.

In Table II, the mean numbers of trials for each group as well as the numbers of avoidance and escape responses are given. According to these indicators, the animals may also be divided into two categories. In experiments with classical pretraining (Group 2) and in some of the animals without pretraining (Group 1a), the total numbers of trials and the numbers of instrumental responses were much smaller than in experiments with escape pretraining (Group 3), escape-classical pretraining (Group 4) and the remaining animals with no pretraining (Group 1b).

It should also be noted that, in the category with the long training, both the number of escape responses and the number of avoidance responses were considerably greater than in the category with short training. This is because in animals with long training, the avoidance response after its first appearance was very irregular as judged from many alternations from shock (escape) to nonshock (avoidance) trials (see Table III).

Table III

The trial of the first avoidance response and number of alternations from shock (escape) to nonshock (avoidance) trials during acquisition and stabilization of avoidance reflex

Group	Pretraining	Trial of the 1st avoidance CR		Number of alternations	
		Mean	Range	Mean	Range
1	no pretraining	13.0	4—23	24.4	8—43
1a	,,	*10.7*	*6—15*	*14.0*	*8—19*
1b	,,	*14.8*	*4—23*	*32.3*	*22—43*
2	classical	4.8	2—10	11,8	7—18
3	escape	15.8	3—44	27.0	22—33
4	escape-classical	8.2	4—20	35.8	27—46

Table IV

The speed of acquisition of avoidance reflex according to different criteria

Group	Pretraining	Mean criterion number according to criterion		
		9 avoid. CR in 10 trials	45 avoid. CR in 50 trials	90 avoid. CR in 100 trials
1	no pretraining	89.4	100.3	10[illegible].7
1a	,,	*34.0*	*37.7*	*41.7*
1b	,,	*131.0*	*147.3*	*152.0*
2	classical	15.8	26.0	19.0
3	escape	77.0	129.0	119.0
4	escape-classical	106.2	132.4	147.2

The high criterion of acquisition of the avoidance CR (90 avoidance responses in 100 consecutive trials) accepted by us is, of course, arbitrary. However, it makes our data relatively independent of the daily fluctuations of the scores. Nevertheless, the same differences between the groups remained when we took lower criteria (see Table IV).

3. Extinction and retraining of avoidance CR

During first trials of extinction, almost all cats behaved very similarly. When the CS did not terminate after the bar-pressing response, the animals showed signs of strong fear and pressed the bar several times until the CS ceased. There was a great variability in the time of disappearance of the avoidance CR and in the number of bar-pressing response during extinction, not only between the groups but between the individuals of each group. As a rule, the bar-pressing responses appeared in the beginning of each extinction session, whereas, towards the end, they disappeared.

After 10 days of extinction, the normal avoidance procedure was resumed and the avoidance CR was retrained.

Table V

The number of the avoidance responses during extinction of the avoidance reflex and retraining period

Group	Pretraining	Number of avoidance responses during			
		100 extinction trials		100 retraining trials	
		Mean	Range	**Mean**	Range
1	no pretraining	47.0	1—92	93.1	89—98
1a	„	*78.1*	69—92	*96.0*	*95—98*
1b	„	*23.5*	1—51	*91.0*	*89—92*
2	classical	69.8	42—98	95.3	94—97
3	escape	35.5	21—50	86.8	84—92
4	escape-classical	39.8	17—58	89.0	84—97

As seen in Table 5, there are clear differences between the groups in the number of avoidance responses during extinction as well as during the retraining period. In cats of Group 2 (classical pretraining), the avoidance CR was more resistant to extinction than in cats of Group 3 (escape pretraining). The data for Group 4, in which the classical pretraining had been introduced after escape pretraining, are very similar to those for Group 3. The retraining of avoidance CR after extinction was quite easy, but it was necessary to apply more shocks in Groups 3 and 4 than in Group 2. Cats of Group 1a, whose performance in the course of acquisition was similar to that of Group 2, retained this simi-

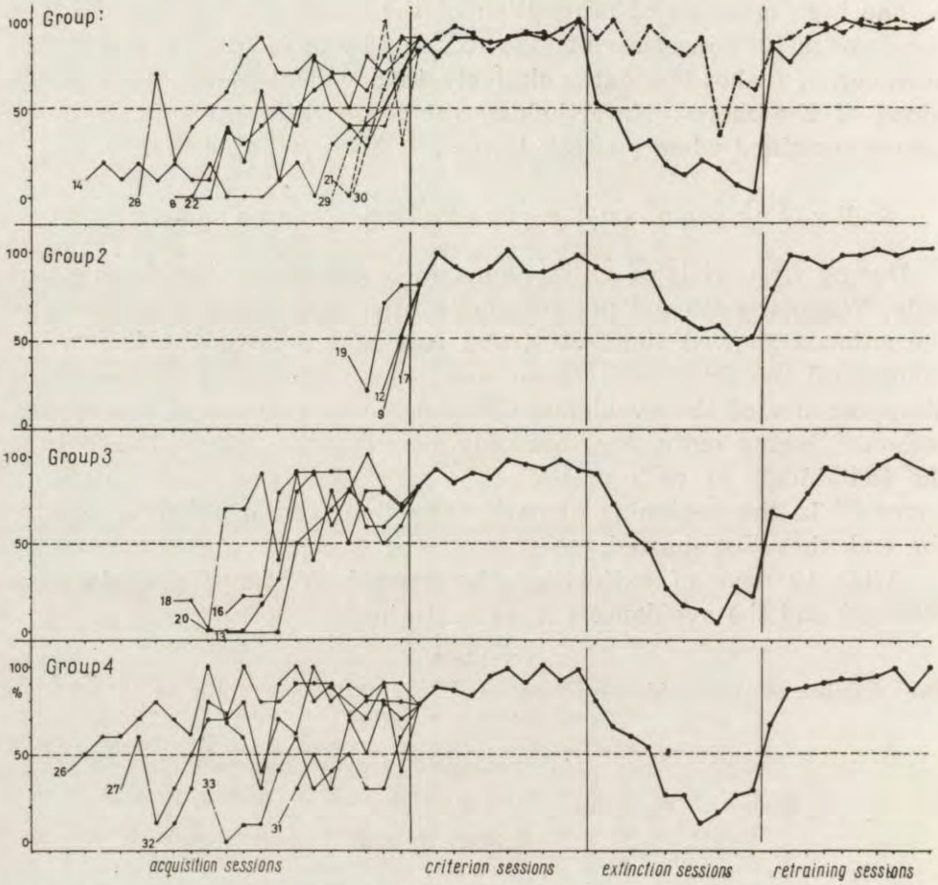

Fig. 1. The course of acquisition, extinction and retraining in different groups of animals.

Ordinates: per cents of avoidance responses. Abscissae: successive daily sessions. Results from acquisition sessions are shown separately in each animal; results from criterion, extinction, and retraining sessions are averaged for each group of animals. By dotted lines the cats of the Group 1a are indicated whereas by the solid lines are indicated cats of the Group 1b and of remaining groups.

larity during extinction and retraining periods. Likewise, cats of Group 1b resembled those of Groups 3 and 4.

The course of acquisition, extinction and retraining for each group of animals is shown in Fig. 1.

4. Latency of the avoidance response

The mean latencies of the avoidance CR (the escape responses are omitted) for each group of animals during 10 experimental days of retraining period are given in Fig. 2. To discover the trends during the experimental session, the latencies were counted separately for successive trials. As seen in Fig. 2, in four out five groups the latencies of avoidance CR became increasingly longer with successive trials. The only exception is Group 1b. The long mean latency to be found in the first

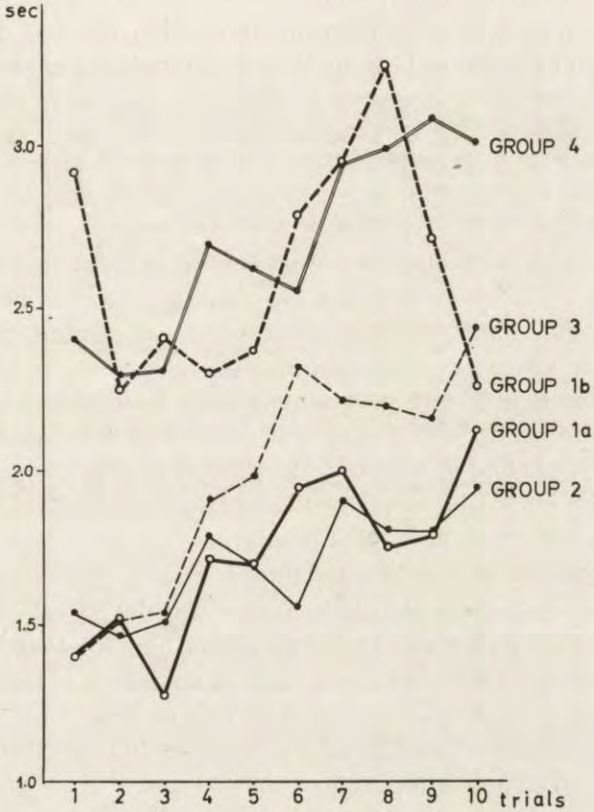

Fig. 2. The mean latencies of the avoidance CR during 10 retraining sessions for each experimental group.

Ordinates: the latency of the avoidance CR in seconds. Abscissae: consecutive trials.

trials in this group was due to only one animal (cat 28) which had very long latencies in the first trial of each session. In the beginning of the session, this cat sat near the door of the cage, and when the trial started it walked to the bar and remained there during the whole session.

What is puzzling in our experiments is that the latency in Groups 1b and 4 is longer than in the other groups, and the consistent drop of latency in the last trials of the sessions observed in all animals of

Group 1b. It is noteworthy that similar results were obtained in 10 criterion sessions before extinction.

Mean latencies calculated for each experimental session show considerable variations in each animal from day to day without any regularity. We did not observe any shortening or lengthening of the latencies of avoidance CR, either during the criterion trials or during the retraining period. When a nociceptive reinforcement was not applied during several sessions, no sign of gradual lengthening of latencies was seen.

DISCUSSION

As seen from our results, there is a clear difference in both acquisition and extinction of the avoidance CR, depending on the kind of pretraining. In animals with classical conditioning pretraining, the formation of the avoidance CR was rapid and the resistance to extinction, considerable. On the other hand, in cats with escape pretraining, the acquisition of the avoidance CR was protracted and the resistance to extinction was small. The animals without pretraining may be divided into two subgroups: one, similar to the group with the classical conditioning pretraining, and, the other one similar to that with the escape pretraining. The group with both the escape and classical conditioning pretrainings was similar to that with escape pretraining.

How are these results to be explained?

As a starting point, we should consider the theory of avoidance conditioning by Konorski and Miller (Konorski 1948, Konorski and Miller 1933, 1936, Miller and Konorski 1928). According to the paradigms of instrumental conditioning proposed by these authors, in avoidance procedure, the CS acting alone is followed by the noxious US, while the compound composed of the CS and the avoidance response is not. In consequence, the proprioceptive stimuli generated by this response play the role of a conditioned inhibitor (CI). The authors suppose that the CI somehow preserves the reflexogenic value of the CS and protects it from extinction in spite of the fact that it is not followed by the US. The experimental evidence, showing that the CI has, in some conditions such a protective role was brought forth by Chorążyna (1957) and Sołtysik (1960). Their experiments have shown that the CS, when used in compound with CI, does not loose its reflexogenic value even after a long period of chronic non-reinforcement.

In consequence, the chain of events in avoidance conditioning may be represented as follows (Fig. 3 cf. Sołtysik and Zieliński 1962). The CS produces the conditioned fear response since it is followed by the noxious US. Excitation of the fear center in compound with CS elicits the movement trained during avoidance procedure. The feed-back (both peripheral and central), generated by the performance of the movement, inhibits the fear center and protects the avoidance CR from extinction. On the basis of this scheme, we can explain the rapid formation of the avoidance CR after classical pretraining. In fact, the external stimulus being followed by the noxious US begins to evoke the conditioned fear response, manifested, among other things, in motor excitement which results in accidental pressing of the bar. Since the electrical shock is not applied, the movement becomes a CI and protects the CS from extinction.

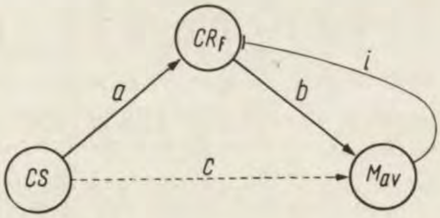

Fig. 3. Schematic representation of hypothetical intercentral relations in positive avoidance reflex.

CS — centre of the conditioned stimulus; CR_f — centre of the reaction of fear; M_{av} — centre of the avoidant movement; $\rightarrow$ denotes: elicits (or excitatory connection); denotes; $\vdash$ inhibits (or inhibitory connection); a — conditioned connection; through which the CS induces the fear reaction; b — conditioned connection through which the avoidant movement is instigated by feat; c — conditioned facilitatory connection through which the CS lowers the threshold in the centre of M_{av}; i — inhibitory conditioned connection. The term „centre" is used here in its functional meaning; it may well be replaced by the term „central excitation".

The question arises why is it that the formation of the avoidance CR is much delayed when escape pretraining is used.

Here a few hypotheses may be considered.

First. According to the results obtained by Zbrożyna (1957), Sołtysik (1960), Sołtysik and Kowalska (1960) and Segundo et al. (1961), when the CI is applied just before the termination of the US, it drastically cuts down the unconditioned reaction. In our experiments, the instrumental movement terminating the noxious US also plays the role of CI and, as such, reduces the strength of excitation of fear center elicited by this US. In consequence, the US is now attenuated by the inhibitory influence of the escape movement. This assumption is evidenced by the fact that, as indicated above, the escape pretraining has a very manifest effect on the general animals' behavior, namely, the cats become much calmer than those with classical pretraining during the intertrial intervals.

Thus, when the CS is followed by the US attenuated by inhibitory influence of well established escape movement, the development of the classical fear CR to the CS is more prolonged and, after establishment, is weaker than that in the previous case. Hence the resistance to extinction of the reflex to this stimulus is weaker.

Secondly. There is now much evidence that recent memory traces produced in any conditioning training are cut short either by inactivation of the cerebral activity in general (ECS, anoxia etc.), or by stimuli producing retroactive inhibition. Because of this the consolidation of the CR is protracted or even impossible. If we assume that the same role is played specifically by strong inhibitory stimuli, the CI established during the escape pretraining and accompanying the end of each trial is the very factor hindering consolidation of the CR and causing its poor development.

Thirdly. Another explanation of the poor development of the avoidance CR after the escape pretraining may be based on the data obtained by Dobrzecka and Konorski (1962). According to these authors, when an instrumental CR is formed to a stimulus which has strong natural bonds with the instrumental response, this reflex being established hinders the formation of the instrumental CR to other neutral stimuli. It seems that an analogous situation exists in our experiments. The noxious stimulus elicits a double effect. One consists in the excitation of the defensive center producing various somatic and autonomic responses. The other effect produced by the specific simulation of the paws by electric shock makes the animal jump, lift his forelegs, scratch the wall, and so on. It is easy to see that these responses are allied with the bar-pressing. This is why the escape response was so readily established in our experimental situation. And so, since the somatic stimulus to the paws becomes strongly connected with the instrumental movement in the escape training its transfer to the neutral stimulus, a tone, is handicaped. The hypothesis stresses the role of the direct connections between the CS center and center of the instrumental CR.

Fourthly. Finally it should be emphasised that the unconditioned noxious stimulus (shock) and the conditioned stimulus signalling it produce non identical central states in the defensive center, since the first one gives rise to pain and the second one to fear. It is possible that in an escape reflex the terminating movement is an escape from pain rather than from fear, whereas, in the avoidance reflex, the terminating movement releases the animal from its own fear reaction (Mowrer and Lamoreaux 1942, 1946, Schoenfeld 1950). The difference between unconditioned pain and conditioned fear may be the reason for a difficult transfer from the escape to the avoidance reflex in animals with the escape pretraining.

It is difficult to say which of these hypotheses is most adequate for our data. The first and the second hypotheses are weakened by the fact that, in our Group 4 (escape- classical pretraining) in the classical pretraining a strong fear CR to the tone was established, but, nevertheless, it did not influence the effect of the preceding escape pretraining. According to the third hypothesis, the escape pretraining may result in retardation not only of the development of conditioned fear CR to the CS (connection „a" in Fig. 3) but also of the direct connection between CS center and center of the terminating movement (connection „c" in Fig. 3). However, the correctness of the third hypothesis should be documented by a different experimental procedure in which the instrumental movement would be not allied with the character of the US.

The results obtained in the animals without pretraining are of special interest. The clear division of this group into two subgroups, resembling the groups with classical or escape pretrainings respectively, shows that for some reasons the course of events was different in various animals. In some of them, first the classical fear CR to the tone was established and, in consequence, the avoidance CR was aquired very easily. In other animals, however, the escape response was first consolidated, and it then determined the slow formation of the avoidance reflex. Whether these differences depend on some purely accidental factors, or whether they reflect the type of the nervous system, cannot be answered yet.

The third and the fourth hypotheses are unable to explain the results obtained in Group 1 irrespective of the source of the division of this group. If the noxious stimulus plays a specific role as a somatic stimulus for bar-pressing response, or if it is some opposition between pain and fear, all of the animals of this group should show similar results to those in the group with escape pretraining. According to the third as well as to the fourth hypotheses, it is logical to expect that if no classical pretraining is used, the acquisition of the avoidance reflex will take a long time, as it did in our experiments. It appears to us that further experiments are needed to answer the question which of the proposed hypotheses, if any, accounts for our data.

To the end this discussion, the results obtained during extinction of the avoidance CR should be commented upon. The resistance to extinction was positively correlated with the speed of acquisition of the reflex. However, it is worth mentioning that during the last hundred trials before extinction the cats of all groups had the same level of avoidance CR performance, i.e., 90 per cent. According to the data given in Table II, the groups less resistant to extinction showed a higher number of escape responses and avoidance responses prior to extinction, as compared with groups more resistant to extinction. Thus, the reason for quick extinction in groups 1b, 3 and 4 may be due rather to a greater number of escape responses during development of the avoidance reflex than to insufficiency of avoidance training. The differences during retraining sessions may be, at least partially, due to different „depth" of extinction in various groups.

SUMMARY

1. The kind of pretraining (classical versus escape) has a definite influence on the speed of acquisition of the avoidance reflex and its resistance to extinction. In animals with classical conditioning pretraining, the formation of the avoidance CR is rapid and the resistance to extinction considerable. On the other hand, in cats with escape pretraining the acquisition of the avoidance reflex is protracted and the resistance to extinction is small.

2. Among cats without pretraining, two groups exist: one group, which is similar to the group with classical pretraining both in the rate of acquisition of avoidance reflex and in the resistance to extinction, and another one, which is similar to that with escape pretraining.

3. The classical conditioning pretraining employed after escape pretraining does not influence the rate of acquisition and resistance to extinction of the avoidance reflex, and cats with such a double pretraining are similar to those in which only escape pretraining is used.

A few hypotheses are discussed.

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IMPAIRMENT OF CONDITIONED DEFENSIVE REACTIONS FOLLOWING LESIONS OF THE LATERAL HYPOTHALAMUS IN RABBITS

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A number of investigators has shown that the hypothalamus is associated with defense reactions. Electrical stimulation of both the medial and lateral hypothalamus in cats and rabbits (Hess 1919, Hunsperger 1956, De Molina and Hunsperger 1959, 1962, Traczyk 1962) evoked fear and escape reactions. On the other hand, lesions of the hypothalamus produced impairment of defense reactions. Wheatley (1944) found that lesions in the medial hypothalamus produced a decrease of reactions to nociceptive stimuli. Most recently, Romaniuk (1962) showed that after small lesions of the medial hypothalamus in the rabbit a marked impairment on defensive conditioned response (CR) occurred: (a), the latency was lenghtened, (b), the CR was often abolished, and (c), the number of intertrial responses decreased. It was interesting to see whether or not the lateral hypothalamus is concerned with defense behaviour. Our preliminary results indicate that lesions of the lateral hypothalamus may impair both escape and avoidance responses (Balińska and Wyrwicka 1961, Balińska 1963). The purpose of the present paper is to study further this problem.

MATERIAL AND METHODS

Experiments were performed on 20 male and female rabbits, about 2 years old, weighing 2 to 3 kg. All of them were trained in avoidance conditioned reflexes. The training was carried out in a wooden cage (1 × 1 × 1 m.), the front wall of the cage was glass to enable observation of the animal. The floor consisted of a grid. In a corner, a small bakelite platform was fixed which could be moved by a gear from a horizontal to a vertical position (Fig. 1).

Training of avoidance conditioned reflexes was carried out by presenting the sound of a whistle (conditioned stimulus, CS) for 5 sec., followed by an electric shock of 40 to 80 V from an AC source. The shock was delivered to the animal's paws through the grid. Escaping from the current, the animal occasionally jumped onto the bakelite platform. At that moment, the conditioned stimulus was discontinued and the current was turned off. When the animal kept staying on the platform, the platform was tilted to force the animal to step on the cage floor. After a number of trials, the animal learned to jump onto the platform as soon as the current was turned on. After several further trials, the animal did the same to the sound of the whistle, thereby avoiding shock. The animal also learned to return down to the floor after each trial.

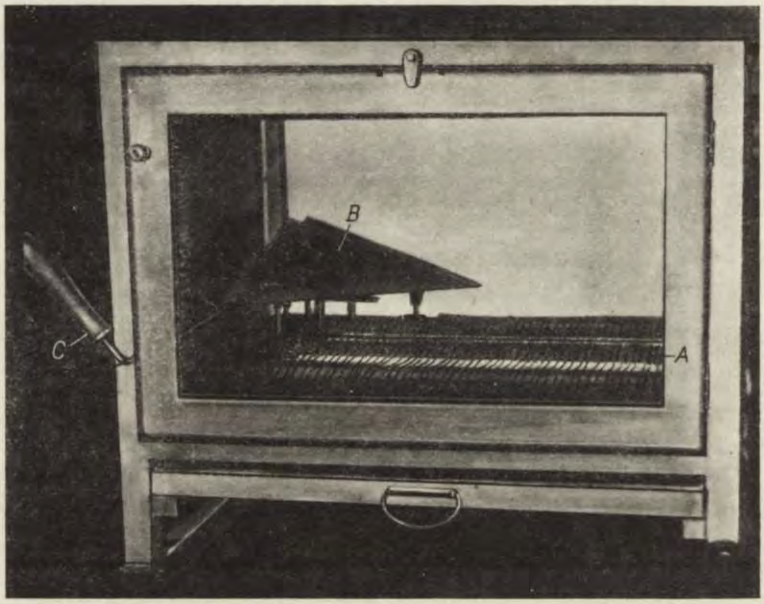

Fig. 1. The experimental cage.
A, grid floor; B, bakelite platform; C, gear to move the platform

Experiments were conducted daily, except holidays. Each daily session consisted of 8 trials seperated by 1 to 3 min. intervals. The response measure was the latency in seconds from the onset of the sound of the whistle to the avoidance reaction. The voltage was adjusted individually, it was 10 V higher than that evoking a treshold reaction. All the rabbits were trained until they reached a criterion of a latency of 3 sec. or less on all trials within 10 successive daily sessions.

After completion of the preoperative training, lesions of the lateral hypothalamus were made bilaterally. The operation was performed under Nembutal anaesthesia (40mg./kg.). Using the stereotaxic atlas for rabbits by Sawyer, Everett and Green (1954), two unipolar steel electrodes, 1 mm. apart, were stereotaxically inserted in each side of the lateral hypothalamus. Electrodes were put into the brain 14 mm. below the surface of the skull, through small holes bored in the skull, about 1 mm behind the coronal suture and 2.5 mm. lateral to the saggital suture. The indifferent electrode was attached to the skin. The lesions were made by passing 3 mA DC current through the electrodes for 20 sec.

Since aphagia was observed for 3 to 17 days after operation, the animals were given 10 ml. of 40 per cent glucose and 100 ml. of saline subcutaneously every day until they recovered their spontaneous eating. Then, the daily training started again.

Two to 3 months after operation the rabbits were sacrificed, and their brains taken for histological verification.

RESULTS

During the first days after operation, all animals exhibited aphagia, a decreased motility and poor reactivity to external stimuli. In 4 rabbits (Nos. 34, 40, 52 and 30), motor disturbances, consisting of „involuntary" deviation of the body to the right, were observed for 3 days.

A few days after operation, reactions to the external stimuli and the motility recovered. During the aphagic period some rabbits showed an „involuntary" chewing behaviour. Three to 7 days after operation, the rabbits began to eat again, but they ate less than before. Rabbit No. 32 started to accept food 7 days following operation. However, 2 days later, he stopped eating for another 10 days. Rabbits Nos. 12 and 33 became aggressive after operation. The aggressive response in rabbit No. 33 consisted of an attack associated with vocalization when someone approached the animal's cage.

Experimental sessions were resumed as soon as the operated animals recovered at least partly their ability to take food. In all the rabbits, marked behavioural changes during testing were found. The avoidance reaction was completely abolished and the escape reaction to the electric shock was absent or decreased. Apparently, the animals showed less fear than before operation. During experimental sessions they were indifferent and tame. They frequently licked their fur or the cage floor. This type of behaviour was rather rarely observed in the preoperative period. The presentation of the CS evoked an orientation reaction with no signs of avoidance. In principle, three types of changes were observed (cf. Table I).

I. Complete or prolonged abolition of the avoidance and escape reactions. In 5 rabbits (Nos. 29, 33, 40, 41 and 45), avoidance and escape reactions were absent for 39 to 90 days after operation. In the first postoperative sessions, the sound of the whistle evoked only a slight orientation reaction. When, after 10 sec., the electric current was delivered, the animals

Table I

Results of lesions of the lateral hypothalamus

Group	Rabbit No.	Time of absence of defensive reaction, type		Time of complete aphagia
		escaping	avoidance	
		days	days	days
I*	29	39	39	5
	33	90	90	5
	40	65	65	5
	41	67	67	7
	45	66	66	5
II	12	5	19	5
	19	7	9	4
	21	7	8	5
	22	7	8	4
	23	8	10	6
	24	6	7	3
	28	7	11	2
	30	7	10	3
	32	14	18	17
	34	9	22	4
	42	8	19	4
	51	5	8	4
	52	9	13	6
III	10	-	9	4
	31	-	4	3

* complete abolition of the defense conditioned reaction was observed throughout the entire observation period.

ran round the cage, squeaking, but they did not jump onto the platform. The CS was then extended to 40 sec. or the shock was increased to 100 to 110 V, but the response did not occur. It is interesting that during the intervals between trials the animals were very quiet and inactive.

With further training, the CS evoked a general motor excitation, but the avoidance reaction was still absent. Rabbit No. 33 became so aggressive that, on the sound of the whistle, it attacked the glass wall of the cage. However, it refused to perform the conditioned reaction.

Histological analysis showed that the lesions were made either in the posterior or in anterior regions of the hypothalamus, 3 mm. laterally (Fig. 2).

II. Transitory abolition of the avoidance and escape reactions. In 13 rabbits (Nos. 12, 19, 21, 22, 23, 24, 28, 30, 32, 34, 42, 51 and 52), a transitory abolition of both avoidance and escape reaction occurred. This effect was, however, observed only for a short period of time (10 days after operation). During the presentation of the CS, the animals ran round the cage and were very frightened, but they did not perform the trained movement. No response occurred even when the electric current was on for 40 sec. After several trials, the escape reaction to the shock reappeared. Initially, this reaction was markedly delayed (it occurred 12 sec. after the current), but, after a few trials, the animal jumped onto the platform as soon as the current was delivered. A few trials later, also

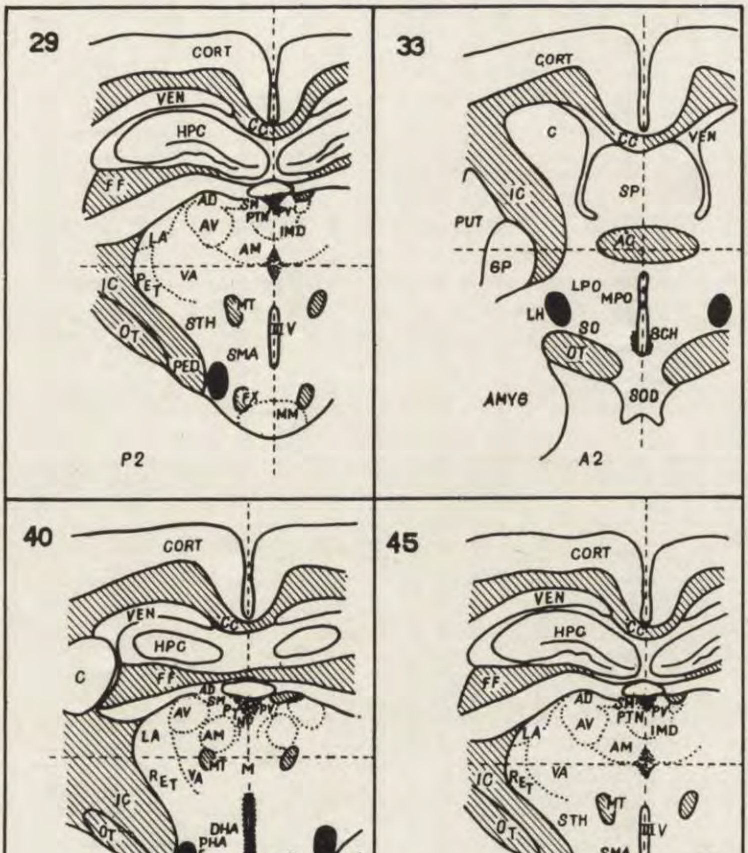

Fig. 2. Diagramic coronal sections of the brains of rabbits Nos. 29, 33, 40 and 45, in which complete or prolonged abolition of the avoidance and escape reactions was found after the lesions of the lateral hypothalamus. Black regions indicate location of lesions.

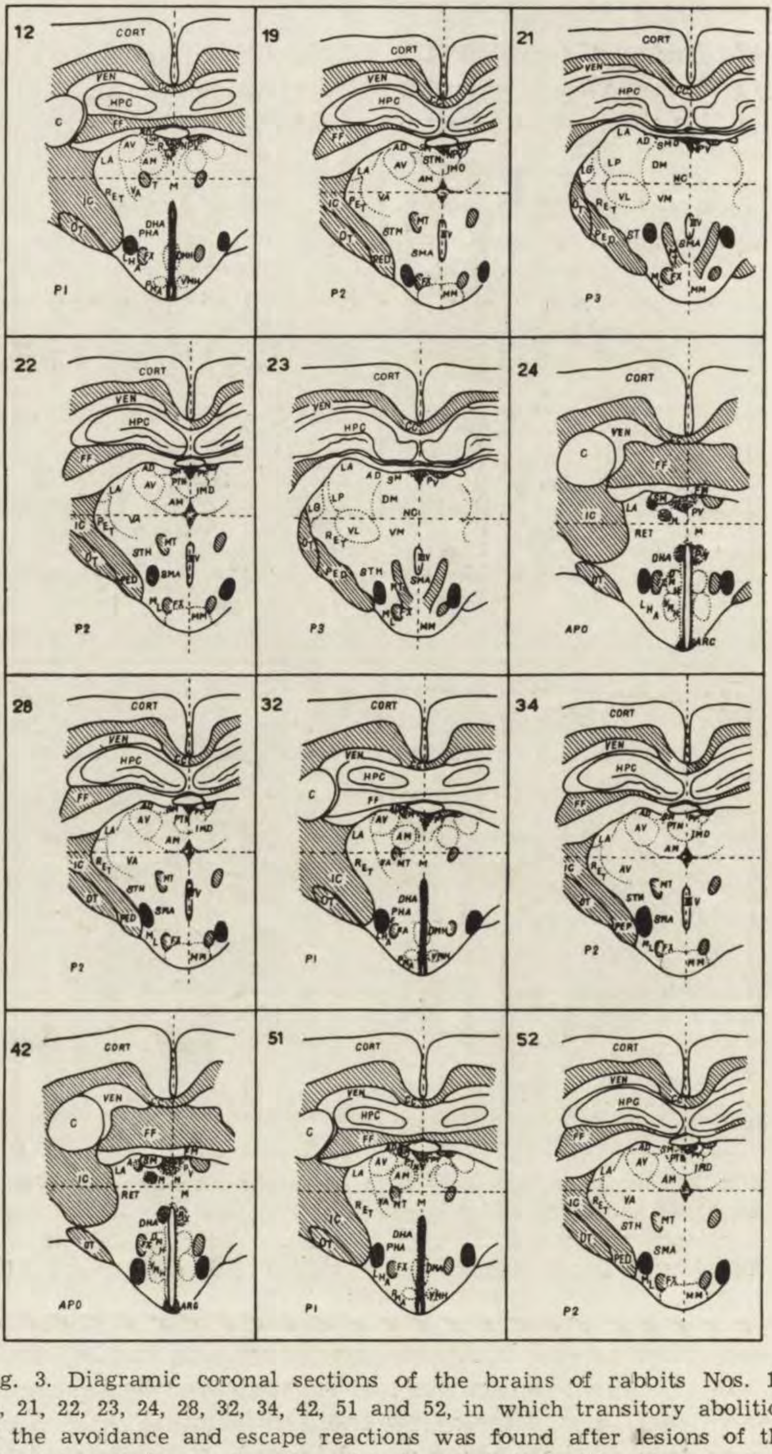

Fig. 3. Diagramic coronal sections of the brains of rabbits Nos. 12, 19, 21, 22, 23, 24, 28, 32, 34, 42, 51 and 52, in which transitory abolition of the avoidance and escape reactions was found after lesions of the lateral hypothalamus. Location of lesions is indicated by black regions.

the avoidance reaction reappeared. The animals were relatively quiet and indifferent during the intervals, except for rabbits Nos. 28 and 30 who became more restless towards the end of the experimental period and performed many intertrial responses. A general impression was that they were more frightened than before operation. In rabbit No. 12, an aggressive type of behaviour was observed throughout the whole postoperative period.

Anatomical sections of the brains of this group are shown in Fig. 3. It is seen that the lesions were placed either in the posterior or in the middle regions of the hypothalamus, 2.5 to 3 mm. laterally (Fig. 3).

III. Transitory abolition of the avoidance reaction. In 2 rabbits (Nos. 10 and 31), the avoidance reaction was absent for only a few days. In response to the presentation of the CS the animals became excited and ran round the cage, but they did not jump onto the platform. Only when the electric current was delivered did the conditioned response occur. The latent period of the response was, however, considerably extended as compared with the preoperative period. After a few days, the animals started to respond to the CS, but only when it was presented for an extended period of time (20 sec.). In such trials, the rabbits performed only a part of the trained movement, stepping with their forelegs on the platform. The latency of this reaction was, however, much longer (5 to 15 sec.) than in the preoperative period (1 to 2 sec.). The rabbits looked very frightened both at the sound of conditioned stimulus and in the intervals between trials. A few days later, the trained movement

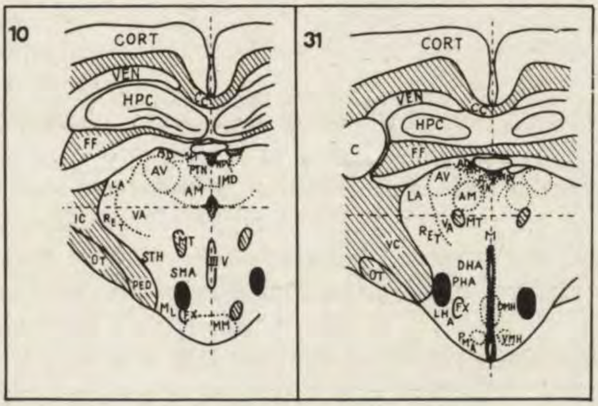

Fig. 4. Diagramic coronal sections of brain of rabbits Nos. 10 and 31, in which transitory abolition of the avoidance reaction was observed after the lesions of the hypothalamus. Location of lesions is indicated by black regions.

of jumping onto the platform reappeared and was repeated many times in the intervals. The rabbits prefered to sit on the platform and, frequently, they had to be thrown of the platform by tilting it down before the next trial.

Anatomical sections of the brains of this group are shown in Fig. 4.

DISCUSSION

Our experiments have shown that limited destruction of the lateral hypothalamus produced both aphagia and a decrease of conditioned as well as unconditioned defense reactions. Impairment of food intake was not, however, paralell to that of defensive behaviour: periods of aphagia, varying from animal to animal, were markedly shorter than those of impairment of defensive reactions. This tends to indicate that the defense type of function and food activities are localized in different lateral hypothalamic regions. It is possible that the reduction of fear and impairment of the escape reaction observed in our group I rabbits might be a result of destruction of the same areas from which electrical stimulation elicits flight reactions. However, in most our rabbits, lesions of the lateral hypothalamus produced impairment of the avoidance and escape reactions only, while the unconditioned reaction to the electric shock remained unchanged. This may indicate to a disruption of the functional intercentral connections concerned with conditioned reactions, which was hypothetized by Wyrwicka (1958). It is also likely that the postoperative deficit may be explained in terms of a damage to the medial forebrain bundle that passes via the lateral hypothalamus (Guillery 1957, Nauta 1958, 1960, 1961). According to Morrison, Barnett and Mayer (1958), and Olds (1958) and Morgane (1961 a, b, c) the medial forebrain bundle plays an important role in „motivation".

SUMMARY

Bilateral lesions of the lateral hypothalamus were made in 20 rabbits in whom an avoidance reaction had been established prior to operation. Following operation, all animals became quiet and showed less fear. In addition, either a permanent or a transient abolition of the conditioned reflex activity occurred. The changes in defensive behaviour persisted considerably beyond the aphagic period that had been noticed during the immediate postoperative period.

The authors conclude that the lesions damaged the lateral hypothalamic structures associated with fear and defense behaviour.

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MULTIPLE REVERSAL LEARNING IN FRONTAL RATS

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It has been proved by the previous paper (Dąbrowska 1963) that the reversal learning of a maze habit is considerably impaired in rats with frontal lesions. While in normal animals, each successive reversal learning requires a decreasing number of trials to reach criterion (Dąbrowska 1959), in rats with frontal lesions, the first, the second and the third reversals are attained at the same rate as during the original learning. It is noteworthy that the prolongation of the reversal training of frontal rats is not due to an increase in the number of both the perseverative and anticipatory errors. A question arises whether the level of the increased capacity to learn, observed in normal animals, is or is not retained by them after frontal lesion.

The aim of the present paper is to answer this question.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments with 10 white rats, all of them 2.5 months old, were made in a four-unit quadruple-choice apparatus, which has been described in the previous paper together with details of the preliminary and main training (Dąbrowska 1963).

Each animal was subjected to an original training followed successively by two reversal trainings. A training was completed when an animal performed six consecutive errorless runs. In each successive task all doors were changed.

Immediately after the third task was mastered, the animals were divided into two equal groups. In group 1, the rostrodorsal parts of the cortex in front of the motor area were bilaterally removed (Fig. 1). The ablations were made by suction under the nembutal anesthesia. In group 2, sham operations were performed in which only the bone, covering the frontal area, was removed. Recovery of animals was uneventful. A month after the operation, the experiments were resumed. Trainings 4 and 5 were applied to both groups (Table I).

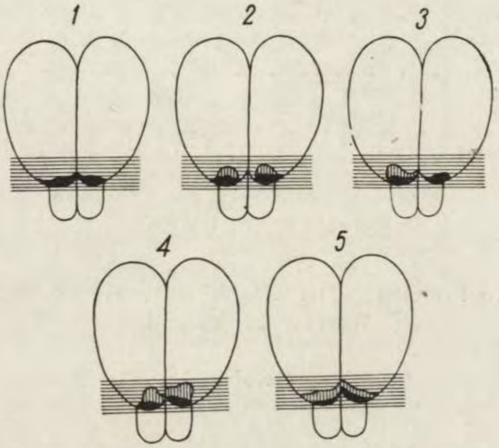

Fig. 1. Brains of the rats with lesions in frontal area
Explanation in text

Table I

Number of runs made in consecutive tasks by normal and operated animals

Group	tasks	1	2	3		4	5
Control	Number of runs for each animals	53	26	17	1 month interval	23	18
		52	26	17		22	16
		52	25	20		22	20
		51	32	21		25	20
		52	31	19		20	18
	mean	52	28	18,8		22,4	18,4
Experimental	Number of runs for each animals	54	26	20	operation and 1 month interval	56	58
		53	31	22		52	52
		53	26	18		51	50
		51	33	20		57	55
		52	31	19		61	57
	mean	52,6	29,4	19,8		55	54,4

After the series of experiments was completed, the animals were killed, their brains removed, fixed in 10 per cent formalin, embedded in paraffin and cut serially. The sections were stained by Nissl technique. Cortical lesions were reconstructed according to Lashley (1932) method. Black spots in Fig. 1 denote the parts of brain from which grey and white substance were removed. Parts from which only grey substance was removed or, in which white substance was slightly damaged, are represented by empty areas.

RESULTS

The results obtained in both groups of rats are presented in Table I. It is clear from this Table that the original, as well as the first and the second reversal learning were almost identical in both groups. Similarly to the data presented in earlier papers (Dąbrowska 1963), the original task required about 51 to 54 trials until criterion was reached, while the second task was mastered after 25 to 32 trials and the third — after 17 to 22.

In contradistinction to these results, considerable differences between groups 1 and 2 were recorded in the animals performance. In control animals, the first training after operation (the fourth task) took 20 to 25 trials, whereas in the frontal group, it required as many as 51 to 61 trials. The second training after operation (the fifth task) required 16 to 20 trials for controls and 50 to 61 trials in the case of animals with frontal lesion.

DISCUSSION AND CONCLUSIONS

A slight decrease in the rate of learning by the control group after a sham operation, can be probably ascribed to the simple fact that there was an interval of 1 month between the pre- and post-operative training. On the other hand, after frontal operation, the decrease in the rate of learning was dramatic since the animals' performance was identical or even worse than that attained during original learning. The rate of the training that followed did not significantly differ from the previous one.

There can be two explanations of the increasing capacity to learn successive tasks by normal animals put into our apparatus. On the one hand, it might be assumed that an increase in the training rate is due to acquiring a certain general capacity to learn, as indicated by Harlow (1949) after his experiments with a learning set. On the other hand, we have presented an ample body of evidence to prove that the increasing capacity to learn is due rather to a normal animal's being able of integrating multiple unit tasks into a complete entity. In our previous paper, we have expressed an opinion that such integration occurs as a result of the function of the frontal or, strictly speaking, premotor cortex.

In our opinion, the latter hypothesis is supported by the data discussed in the present work. In fact, since after the destruction of the frontal region, the animals' performance returns to the state recorded during their original learning, they are no more able to integrate the maze habit into a complete entity.

On the contrary, it seems more likely that, if the rats acquired a certain general knowledge how to learn, this knowledge would be identical in character with that required for the last pre-operative task.

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STUDIES ON THE STAGES OF SPATIAL ORIENTATION IN FEMALE *BEMBEX ROSTRATA* (LINNÉ 1758) RETURNING TO THEIR NESTS (*HYMENOPTERA, SPHEGIDAE*)*

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To the memory of Jean-Henri Fabre
on the 140th anniversary of his birth.

The observation of many flying animals leaving their nests and returning has long given the impression that their orientation in terrain is not uniform along the entire route. This divergence is manifested, if only by the differences in the character of a flight, in respect both to its ceiling and complications in its route. The latter has already been described by Bates (1863, p. 33) who examined *Microbembex monodonta's* (Say)[1] flights, it had made after leaving the nest. He defined the purpose of these flights as "for taking note of the locality". This sort of flight of numerous Hymenopterons was also described by Peckhams (1898) who called it „locality studies". The same term was used by Raus (1918). Ferton (1909) mentioned them as „exploration du terrain". A now commonly used name, *orientation flight*, could already be found in von Buttel-Reepen's work (1900, pp. 177—193 "Orientierungsausflug") and later it was used by other re-

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[1] Treated by him as *Bembex ciliata* Lep.

search workers, such as, Rau (1929, p. 43—44, "flight of orientation"), Frison (1930), "orientation flight"), Tinbergen (1932), Weyrauch (1935) and Nielsen (1945, p. 151, "vol d'orientation"). Van Iersel (1952) also calls them "re-orientation flights". Less attention was paid to flights made near the nest by insects returning to it. The lack of any commonly accepted name for defining such flights, emphasizes this fact. Opfinger (1931) spoke simply of "arrival flights", van Iersel called them a "hesitation". In the present paper, we shall call them, *recognition flights,* which seems accurate enough to determine the heart of the matter.

Actually, on the basis of analysing the behaviour of animals from the standpoint of their spatial orientation, various research workers came to the conclusion that the route from or to the nest can be divided into several *stages*. Such a division into three stages for bumblebees was thus made by Wagner (1907). Shortly afterwards, two stages, the *proximate* and the *distant orientation,* were distinguished by Watson and Lashley (1915) in the spatial orientation of birds, while Rabaud (1927), also using the example of *Aculeata,* but this time with honeybees, distinguished: 1) a flight to the nearest surroundings of the nest, 2) a recognition of the locality and 3) a recognition of the nest.

Each division of such a type must be based on a certain definite criterion. The manner of orientation served as such a criterion in the case of Watson's and Lashley's division. — In the stage of a proximate orientation — in contrast to the distant one — an animal directs its movement by stimuli coming directly from the destination place of its flight, for instance, the nest. In his division, Wagner takes into consideration two factors. One is the characteristic orientation flights of bumblebees who, within (1) "vision range", 1.75 m. in radius, fly away backwards with their heads pointed towards the nest, while within (2) "discernment range", up to 10 m. in radius, make their orientation flight in a forward position. A manner of orientation is another factor, since — according to his opinion — within the discernment range they discern more details on the ground than within (3) the last, outermost range. He believes, therefore, that finding the nest depends on the properties of the surroundings, that is, the "indication points". The difference in orientation in particular stages would primarily consist in the number of optical features of the surroundings used, and in the manner of seeing them. Rabaud's division is also based on two factors. One of them is the character of a flight, stages 3 and 2 being at a relatively low ceiling often taking the form of curves; the outermost stage 1 or, the so-called "ligne d'abeille" is a straight line flight usually made fairly high above the ground. The mechanisms of spatial orientation (general knowledge of the terrain — in the third stage; other, nearer and more detailed stimuli — in stages 2 and 1; there are also differences occurring between the latter two stages) is another factor.

Although Wagner's and Rabaud's divisions are based on inconsistent criteria, they can be applied to a great many flying *Hymenoptera*. On the other hand, Watson's and Lashley's division, however it might tempt an investigator by its univocal fundamental principle, cannot usually be applied to *Hymenoptera*. It is true that there are instances of insects that — in the vicinity of their nests — make for them, guided primarily by stimuli of these nests that they feel. For instance honeybees (Kathariner 1903) or *Halictus duplex* Dalla Torre (Sakagami and Hayashida 1961), are guided by the smell, *Philanthus triangulum* (F.) — by the sight of a spot of sand unearthed from the burrow and, *Odynerus* (*Ancistrocerus*) *parietinus* (L.) (Molitor 1939a), *Megachile* Latr. (idem, 1933, 1937b), *Halictus* Latr. (Sakagami and Hayashida 1961), *Cerceris* Latr. (cf. Marquenie 1954) — by the sight of the opening of the burrow itself. In general, however, *Aculeata* guide their movements near the nest by environmental properties, using them as orientation marks, while the stimuli, coming from the nest itself assist only at short distances (Rabaud 1927, Carthy 1954, 1956, Chmurzyński, in press a).

In the present paper, the differences occurring in the mechanism of spatial orientation or, at least, distinct differences in the behaviour such as, for instance, the dissimilarity of the flight character, etc. have been adopted as criteria for dividing the return to the nest into individual stages. Retaining for the first two stages, corresponding with Rabaud's stages, the names introduced by Watson and Lashley, which have already won a place in science — provided that we shall not stick slavishly to their criterion of division — it can well be stated that the following stages should be distinguished in spatial orientation of flying *Hymenopterons:*

1) finding the site of the nest, a *distant orientation,*

2) recognition of the surroundings of the nest, a *proximate orientation sensu lato,*

3) finding the nest entrance, an *immediate orientation,*

4) recognition of the nest,

5) orientation inside the nest.

Obviously, in spite of the criterion, established above, this division — in the same way as Rabaud's classification, has to a certain extent a descriptive character. Considering, however, the diversity of the orientation mechanism of various insects, there can be no other posibility. Of course, not all of stages mentioned above, occur in all species of animals. It seems, however, that the distinction of stages 3-5 not only fail to present difficulties in practice, but conversely play a positive, cognitive role and leads the researcher to examine the mechanism of orientation in these phases. This cannot be said of the initial phase. A differentiation by force of two stages (1 and 2) if there are no distinct ethological grounds for it (for instance, different character of the flight, different mechanism of orientation, etc.) is, in my opinion, ill-founded. Usually, however, adequate premises exist for doing so.

A determination of the character of the return of *Bembex rostrata* (Linné 1758) female specimens to their nest, examined from the point of view of stages in the spatial orientation of these insects, constitutes the subject of the present paper. The division, described above, will be used for this purpose.

When we consider an animal returning to some place, we have to take into account two elements, a biological and a physical one; the latter could be even defined as geometrical. Only these two, taken jointly, can present a full picture of the return of an animal. Analysing successive stages of the *Bembex*' spatial orientation during her return to the nest, we shall, therefore, concern ourselves with a field of orientation in a given stage and, its biopsychological mechanism.

The concept of a *field of orientation* is geometrical in character and it determines a field over which an animal manifests its orientation capabilities, in a sense adopted in the present paper, that is, its capabilities of recognizing the place and finding the way to the nest. They are manifested in a certain characteristic manner. Thus, the field of orientation corresponds to a certain stage of orientation. A change in the behaviour, or in the character of orientation of an animal coming back to its starting point, is decisive for the beginning of another stage and, at the same time, it is decisive — in a geometrical sense — for the limit of the field of orientation of the previous stage. In the light of the problem constituting the aim of the present work, materials concerning the mechanism of the *Bembex*' orientation in particular stages, are quoted in order to characterize these stages, and not to give an exhaustive answer to the question, which is really the orientation of this wasp in successive phases of its return trip. Only the return to the nest and, in addition, only the first three stages of it, were subject to analysis.

The entire field of orientation, which, in theory, surrounds the nest radially, can be either externally unlimited or have boundaries, because — and this should be emphasized — it is not equal to a range of the terrain known to an animal. Since a field, in which an animal can find its destination point, that is — within the scope of the present work —

its nest, is accepted as a field of orientation, this field can: 1) exceed the limit of an area known to an individual, in animals having a topographical type of orientation which occurs in insects, and 2) have no outer limit at all as, for instance, in the animals with orientation of the astro- and helionavigational type, such as birds (cf. Wojtusiak 1948, 1949, 1960, Matthews 1955).

There is no doubt that the return to the nest by stages is, to a certain extent, correlated to ranges, distinguished by ecology on the basis of the degree of the psychological attachment of animals to their terrain. Usually, the following three *ranges* are distinguished: 1) *territory,* 2) *home range,* and 3) *life range* (cf. Burt 1943, Griffo 1961). Now, in animals having their own territory, it could correspond to a field contained within the outer limits of the field of proximate orientation. The stage of distant orientation would stretch over the first two ranges and even somewhat beyond. Thus, for instance, Baerends (1941) maintains that the boundary of the field of distant orientation of *Ammophila pubescens* Curt.[1] is located twice as far from the nest as the boundary of the area known to the wasp (cf. reference 5 for Table II). The possibility of the existence of sub-stages in the distant orientation should, therefore, be considered. It is also as a rule — as Griffo (1961) believes, with reference to the cotton mouse *Peromyscus gossypinus* (Le Conte) — that beyond its life range, an animal's movements are a matter of chance, while within its life range, it moves in a predetermined manner, when it makes for its home range. The orientation within the latter range is also likely to have certain definite patterns.

Distant orientation

It is quite obvious that any analysis of distant orientation must be preceded by answering the question as to whether this stage of orientation actually happens at all with a given animal species.

An impression is formed, by preliminary observations of the female *Bembeces* returning to their nests, that there is no need to distinguish the first two stages of their return. Such a differentiation seems to be baseless. The situation observed is drastically different from that of a honeybee coming back to her hive and even more different from that presented by *Cerceris* Latr. (cf. Fabre 1879, Peckhams 1898). Unlike the others, the *Bembex*' flight does not show any differences in the height of the ceiling. In her movements, a low ceiling, long-distance flight can be distinguished, sometimes as long as 10 m. from her nest

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[1] A form examined by Baerends under the name of *A. campestris* Jur. has been classified by Olberg (1959, p. 12) within this species.

and, in fact, passing without any change in its character into the trip to her feeding or hunting ground. In the same way, short flights, similar in character to those mentioned above, when the *Bembex* makes for wild thyme, only a few meters away, can be observed as well. These flights take place at a ceiling of about 30 cm. (cf. Chmurzyński, in press b). The same applies to the routes covered by the *Bembex* flying back to her nest. This, I believe, provides a basis for the impression that the character of the *Bembex*' visual orientation, is in principle approximately identical along the entire route. It should be readily expected that the further the distance from the nest, the more general becomes the knowledge of a terrain. Perhaps a certain role might be ascribed here to such topographical features as shrubs, roads, etc. The observations of the *Bembex*' departures along the roads or, of her very frequent habit of flying above paths, even in plain, grassy terrain, in this respect resembling the dragonflies of the family of *Aeschnidae,* which keep flying along forest vistas, can provide some proof of this theory. It is quite possible that with the *Bembex* this habit is correlated with the territoriality (cf. Kormondy 1961).

The *Bembex*' possession of a generalized knowledge of more distant areas (in addition to a possible knowledge of details) is suggested by her flights made at higher ceilings, which I have occasionally observed. However, I do not mean mating or hunting flights. In 1951, I observed one such case on a sandy sport ground almost devoid of grass, when an insect, after leaving its burrow and being disturbed by something, soared by spiral flight, resembling *Cerceris* Latr.'s orientation flight, climbed to a ceiling of a few meters and, subsequently, flew away. Another time, it was on a sandy forest clearing, covered with sparce grass. A specimen of the *Bembex* took off, flew to a distance of about 60 m, gradually climbing to an ever higher ceiling, that is, to approximately 3 m. and, after some time, disappeared from my field of view. Another *Bembex,* leaving a definitely closed burrow, at first, soared high to a ceiling of 2.5 to 3 m., then flew low around and above the surroundings of the nest, alighted, camouflaged the entrance and, once more, took an orientation flight at a ceiling of 3 m. Once, a B_{102} specimen[1], released behind tall trees and a one-storied cottage (cf. test 1, below), flew close to the roof of the house, that is, about 6 m.

A closer observation, particularly of the *Bembex*' behaviour, induced by a change in the neighbourhood of its nest, when orientation and re-

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[1] *B* serves as a symbol of *Bembex rostrata* (L.) ♀. The successive specimens examined since 1951 were given successive numbers, for instance, B_1, B_2, etc. (cf. Chmurzyński 1953, p. 29).

cognition flights appear, alters the picture of an uniform return to the nest. It becomes quite similar to that observed in bumblebees by Wagner (1907) who based the concept of the range of vision precisely on the occurrence of the flights mentioned above. Incidentally, bumblebees also make extensive orientation or recognition flights only in exceptional cases (cf. Frison 1930). Other manifestations of the *Bembex*' specific behaviour near the nest which can serve for determining an external boundary of the field of proximate orientation, provide still another proof of the separateness of the distant orientation of this insect. Obviously, this boundary is, at the same time, an internal boundary of the field of distant orientation and indicates the preciseness of orientation at this stage.

A range of distant orientation, separate from that of proximate orientation different, if only — as in the case of bumblebees — by the extent, by the accuracy of the knowledge of a route, by the size of the orientation marks discerned by an insect and by the fact that, in principle, no orientation and recognition flights are recorded, can and should be, therefore, distinguished in the spatial orientation of the *Bembex rostrata* (L.) ♀.

The field of distant orientation, corresponding to this stage, theoretically surrounds the nest in all directions, beginning a certain distance from it, that is, from the external boundary of the field of proximate orientation. In practice, the *Bembex*, like other animals with topographical orientation has a field of distant orientation that is not necessarily round and differs from such a shape to an extent depending on the distribution of orientation marks.

It does not seem likely that authors of investigations on this subject realize, what is, in point of fact, the outer boundary of the field of distant orientation. Generally speaking, there can be two meanings of this term.

The first would be a boundary of the field of orientation of a particular specimen in a given time and for a given nest. As such, this boundary would be marked by a line, connecting points most distant from the nest, but from which this animal could still manage to find its way back. This definition is, however, altogether "unworkable", because such a line cannot be traced, since finding even one point located on it would necessarily result in losing the specimen.

A mean boundary — another meaning of the external boundary — does not evoke such reservations. In this case, two possibilities exist.

A more concrete result can be obtained by investigating the maximum distance covered in the return trip by several insects of the same species that live in the same group of nests, which should be as close together as possible. This, however, in the case of rarer species, is sometimes impossible and, consequently, specimens must be investigated on various sites which will give an average specific boundary. Of course, effort should be taken to see that the habitat in all cases is as similar, ecologically, as possible. An example of such an investigation was given by Fabre, (1882, pp. 98—123) who studied mason bee, *Chalicodoma muraria*

(Retz.) His results were interestingly analyzed by Bouvier (1901), who found that the ratio of the number of insects returning to their nests with the number of insects released far from the nest falls constantly with the increase in the distance at which they were released:

— with the distance of 2.5 km. in a flat terrain, the ratio of returning insects is as follows:

$$\frac{4 \text{ to } 4.6}{10} \text{ or, } 0.4 \text{ to } 0.46;$$

— with the distance of 3 km under similar terrain conditions:

$$\frac{3.5}{10} = 0.35;$$

— with the distance of 4 km. in hilly terrain:

$$\frac{2.25}{10} = 0.23; \left(\frac{2.62}{10} = 0.26 \text{ might be expected for an even terrain}\right).$$

It is, however, not simple even in such a case as this; not even theoretically. At a given and quite sufficient level of significance, for instance, 0.05, our boundary, statistical in character, should connect points with number of returns equal to 0. This is, however impracticable. It would be much better to examine the boundary of a "partial return" (e.g. of 50 per cent of insects), but even this would still present serious difficulties in practice, which is easy to understand, even if we intend to examine this distance only in the four main directions from the nest[1], since it would be necessary to have at our disposal a great many specimens, which in the case of such solitary insects, is rather difficult sometimes.

It is generally understood that 20th century patrons of sciences, perhaps in all countries of the world, in their belief that quantity will pass into quality, demand rapid and abundant results of scientific studies. It is, therefore, ever more difficult to find papers on the distance of the return so well documented as those of Fabre. Instead, they are conducted, in practice, with the application of the third criterion, that is, the distance from the nest is considered from which even the lone specimen released fails to return (cf. Molitor 1935, 1936, 1937a, b, 1939 a). The specific property of this method should be kept in mind. Probability of homing of an animal from the life range is 100 per cent, whereas without its limits probability of going towards the known area and consequently

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[1] Here is a short calculation. First, we must find the distance, from which a specimen released will fail to return to its nest (and, therefore, one is already lost) and, at this distance, to release, for instance, another 9 specimens. Suppose That this is the distance that 70 per cent of the specimens return (2 more lost). We move further and once more release 10 specimens. Even if we succeed in finding at once the boundary of return of 50 per cent of the insects (5 more lost), the total number of specimens lost in examining this boundary, in one direction only, amount to 8; to examine it according to this scheme, we must have, therefore, 13 specimens and — in all the 4 directions — 28 specimens.

finding the nest itself declines rapidly to a half of this value and subsequently amounts $\frac{\alpha}{\pi}$, where $\alpha = \mathrm{arc\ tg}\ \frac{a}{l}$. In the case of theoretically perfect circular shape of the life range a is a half of the chord joining the tangential points of two straight lines drawn from the point of release of

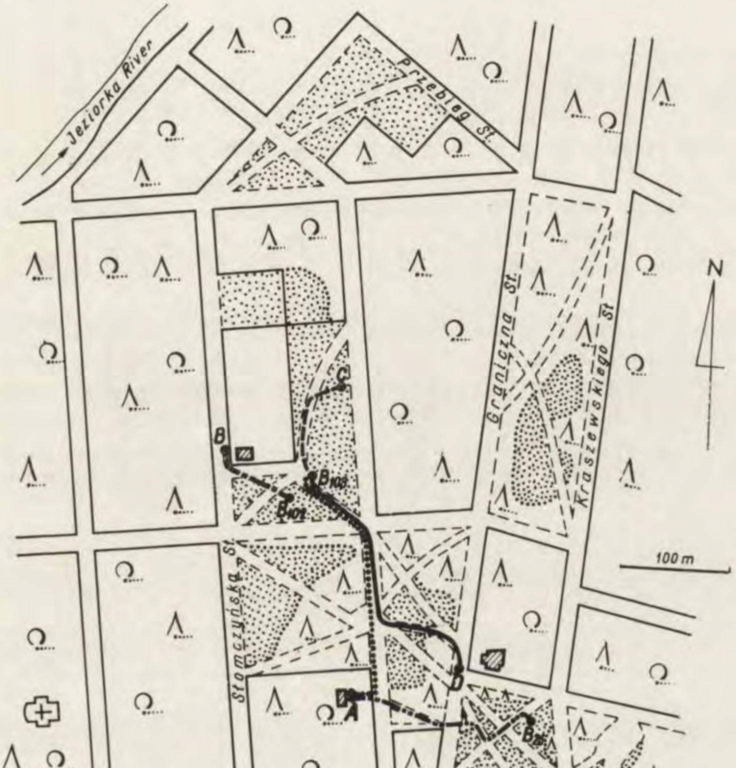

Fig. 1a.

Site diagram for experiments concerning distant orientation of B_{25}, as well as B_{102} and B_{103}, made at Skolimów-Konstancin. Only some buildings are marked. Open fields, marked by dots, the remaining terrain is a mixed forest.

The wasp B_{25}, after being taken behind a row of pine trees, a street, a young pine tree forest and another street, was let go at point A, at a distance of 150 m in an air line from the nest. The wasp B_{102} was carried from point B_{102}, denoting the nest, along a marked route to point B located behind some tall trees of a park and a one-storied house 75 m. in an air line from the nest.

The wasp B_{103} was released at point C at a distance of 100 m., from behind a sandy forest clearing, at point A at a distance of 200 m. and at point D at a distance of 265 m. behind a road with two rows of pine trees, a clearing and a row of pine trees in Graniczna Street. It was released in the middle of this street.

an animal with the circumference of the life range (the value a grows with the increase of the distance between the release point and the limit of the life range); l is a segment between the release point and the above mentioned chord — perpendicular to it. At the distance of about one and a half radius of the life range from the nest the animal's chance to start

Fig. 1b.

Site diagram for an experiment dealing with distant orientation of B_{201} made at Skolimów. Denotations — identical with those in Fig. 1a. The wasp was taken to point E 500 m. in an air line away from the nest from where, let loose, it returned.

in the direction of nest and to find subsequently the nest amounts 25 per cent. The probability of this declines down to 5 per cent only at the distance of six radii of the known area from the nest. It follows from the above considerations that the positive results of homing of a single individual fail to provide evidences for defining a radius of the life range. On the contrary, the negative result speaks in favour with a great probability that an animal has been released beyond the life range. In this possibility of finding the radius of the life range of an animal consists the value of this method. Since in Poland the *Bembex* is a rather rare[1] insect, and the author of the present paper is not free from the stress of now predominating customs, he contented himself with finding the nearest point from which the first specimen of *Bembex rostrata*

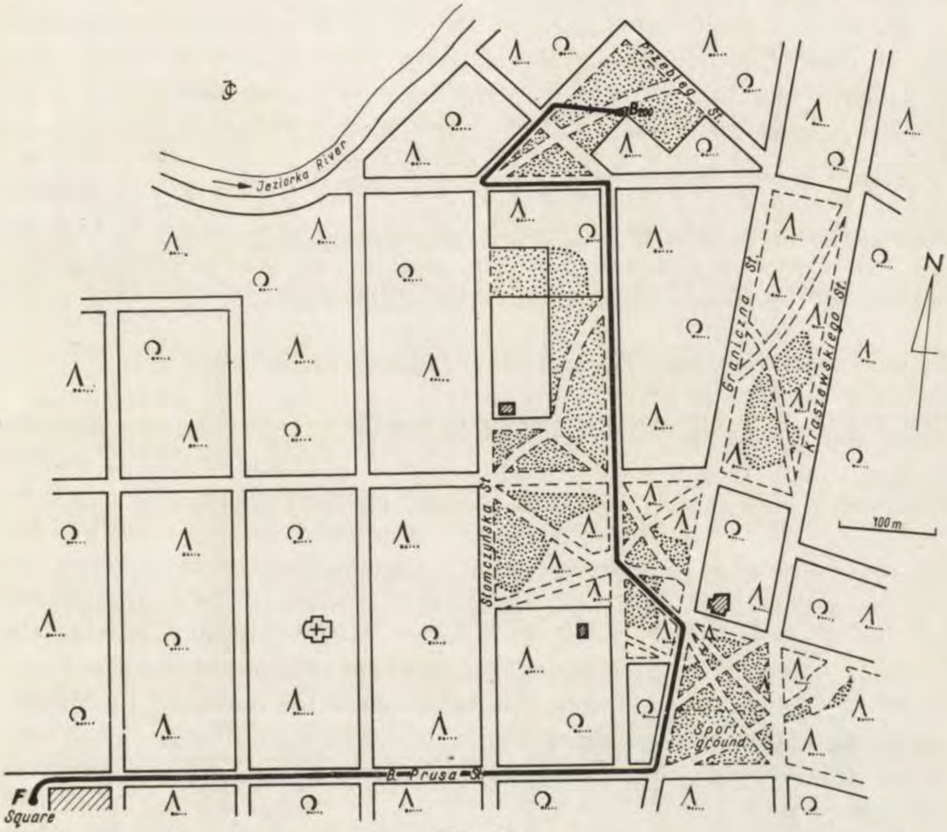

Fig. 1c.

Site diagram for an experiment dealing with distant orientation of B_{200} at Skolimów. The wasp, carried along the route marked and let loose at point F on a square, separated by an extensive part of the settlement with many trees, from a system of fields devoid of trees between Przebieg, B. Prus, Słomczyńska and Kraszewski streets — did not return to the nest.

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[1] The author was compelled to face and fight this difficulty in his work on the spatial orientation of this species conducted in the neighbourhood of Skolimów-Konstancin, Izabelin, as well as of Świder near Otwock (Warsaw Voivodship). The papers by Minkiewicz (1931, 1933) fail to indicate that *Bembeces* occur in colonies at Mądralin (the vicinity of Mlądz near Otwock) and at Sadowne (Węgrów District, Warsaw Voivodship). These incidences, on the territory of Poland, namely,

(L.) failed to return to its nest. Perhaps there is no need to add that here we have had to do with a zone of boundary and not a definitely drawn line of boundary. In view of the lack of sufficient information, even these data give us a certain indication on the problems we are interested in.

Test 1 consisted in trapping close to the nest, marking, transporting an insect in a closed container and releasing it some distance away. In six experiments made with B_{25}, B_{102}, B_{103} and B_{201} in the neighbourhood of Skolimów-Konstancin, female *Bembeces* returned to their nest in a straight line flight from distances of 75 m., 100 m., 150 m., 200 m., 265 m. and 500 m. (Figs. 1 a, b). B_{212}, released at Izabelin from behind a young, dense pine-tree forest about 2.5 m. high did not return from a distance of 700 m. and B_{200} at Skolimów-Konstancin, did not return from a distance of 900 m. (Fig. 1 c).

Proximate orientation

At the end of the first stage of its return to the nest, the *Bembex* reaches the external boundary of the field of proximate orientation. The observation of the orientation and recognition flights constitutes the first premise which — as we have already mentioned above — entitles the investigator to distinguish the stage of proximate from distant orientation of female specimens of *Bembex rostrata* (L.). This is the first, simplest and, at the same time, the least accurate method of investigating the external boundary of the field of proximate orientation. In the same way as the remaining methods, this one differs from the means of investigating the boundary of the field of distant orientation, insofar as it facilitates the studies of individual properties, characteristic of a given specimen and a given nest.

This method was applied in the following manner (test 2). Since under normal conditions, apart from the early period when building her nest, the *Bembex* does not undertake any extensive orientation or recognition flights, she was prompted to do so by disturbing her orientation, that is, by changing the situation near the burrow. As already observed by van Iersel (1952), an orientation, as well as recognition flight, are the responses of an insect to the change in the situation near its burrow, noticed on its return to the nest. It has been proved by the results of my experiments (unpublished) that an orientation flight can be also incited

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in the neighbourhood of Łękowo near Grajewo (Białystok Voivodship) were recorded and reported only by Bischoff (1927, p. 202). Besides, these colonies probably do not exist now, in the same way as the open sandy wastes on which Minkiewicz' experiments were made, are no longer available.

by a change in the surroundings perceived by an insect when leaving its burrow.

In addition to experiments of this type made especially for this purpose, the observations of the orientation and recognition flights, carried out on the occasion of other experiments, were also taken into account. The range of these flights usually reached a radius of about 2 m. Sometimes, however, flights were also observed covering longer distances, even as far as 10 m. from the nest. If we collect distances of particular orientation flights with radii exceeding 2 m., an illustration is obtained (Table I) of the most frequent maximum range of these flights. Since distances exceeding 3 to 4 m. are not reached in flights represented by regular, symmetrical lines, it might be assumed that, during their orientation flights, the *Bembeces* inspect a field approximately 6 to 8 m. in diameter. This can also be concluded on the basis of the observation of recognition flights.

Table I

Wasp	Distance in m.	Wasp	Distance in m.	Wasp	Distance in m.
B_{70}	2.0	B_{186}	3.0	B_{131}	5.0
B_{183}	2-3	B_{196}	3.0	B_{204}	5.0
B_{197}	2.5	B_{220}	3.5	B_{137}	5-6
,,	3.0	B_{191}	3-4	B_{206}	5-6
,,	3.0	B_{90}	4.0	B_{186}	6.0
B_{188}	3.0	B_{196}	4.0	B_{70}	10.0
B_{192}	3.0	B_{108}	5.0		

Data important for this study are sometimes obtained as a "by-product" of the "choice" training experiments which consist in supplying an insect with elements of a training system contrasting with each other and distributed separately at the sides of a burrow (Tinbergen 1932, Tinbergen and Kruyt 1938, Chmurzyński 1947, 1953, 1960). Sometimes, it happens, that after an experimental system is distributed, a confused *Bembex,* who cannot find its burrow, begins to work off her excitement by abortive digging in various places, usually changing suddenly every now and again. Now, the range of this activity, in principle never far from the place in which the burrow is situated and extending within a radius of about 2.5 m. from it, is always located within limits of the field proximate orientation. This makes it clear that the orientation of a wasp, in this situation, is based primarily on landmarks that are distributed within the field of distant orientation.

In both these methods, we have to do with a rough estimate of the boundary of the proximate orientation field. The first, based only on an assumed assessment of the range of flights, which after all might exceed the range we are interested in, could possibly yield numbers that would be too high. The second — contrarily — can lead to a mistakenly diminished range of the field. The third, training method of estimating external boundaries of the proximate orientation field, although somewhat similar to the former, is superior in regard to accuracy. When, after some training with a system applied in the Tinbergen and Kruyt (1938) type experiments, the system is shifted upon the return of an insect in various directions and to various distances, then the distance can be found, beyond which the insect will not alight in search for the entrance to the burrow (test 3).

Such an experiment was unintentionally carried out by Fabre (1879, pp. 275—292), who shifted a stone with a nest of the mason bee, *Chalicodoma muraria* (Retz.) attached to it, a distance of 2 m. away. The mason bee did not now pay any attention to the nest, instead she began an intensive search in the neighbourhood of the original place. However, when he moved the stone a distance of 1 m. only, sooner or later the insect alighted on the nest (in the same way as the bumblebees in Free's experiments, 1955). Clearly, then, in that concrete case, e.g., precisely with that species, with this specimens, in that place and in that particular direction from the nest, the range of the proximate orientation field of the mason bee reached 1—2 m. This was not found by Fabre, if only for this simple reason that his experiment was made seventy years before the division of spatial orientation into stages was introduced (vol. 1 of "Souvenirs entomologiques" was prepared about 1856). The same method was put into use by Tinbergen (1932) who deliberately applied it to the bee-killer wasp, Philanthus triangulum (F.).

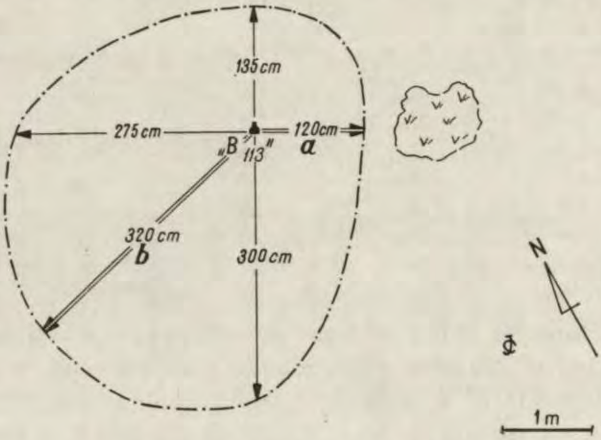

Fig. 2a. Drawing of field B_{113}

Fig. 2a — 2e. Diagrams of fields of proximate orientation, prepared on the basis of the training "shifting" experiments. They are oriented in relation to the axis of the burrow vestibule.

Test 3 was made on 7 female specimens of *Bembex rostrata* (L.). In two cases, a twig, to which a trained wasp responded, was shifted from

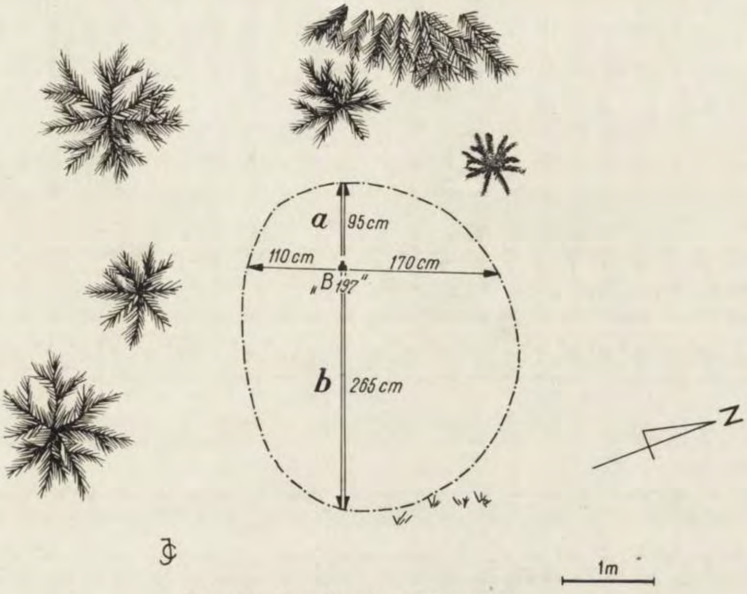

Fig. 2b. Small plan of field B_{197}.

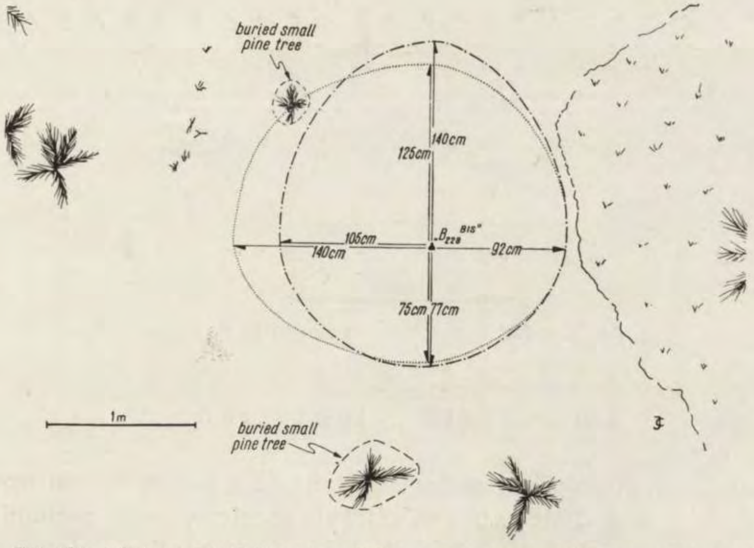

Fig. 2c. Results of two experiments of the same type with B_{228}. These limits were obtained after covering with sand two small pine trees about 30 cm. high.

the nest for topographical reasons in one direction only; in the remaining tests it was moved in at least four directions. The wasps followed that twig up to a distance of 3 m., but at a distance of 5 m., they did not react to it. In the remaining cases, presented in Figs 2a—c the limits of the proximate orientation field were obtained, reaching to 3.5 m.

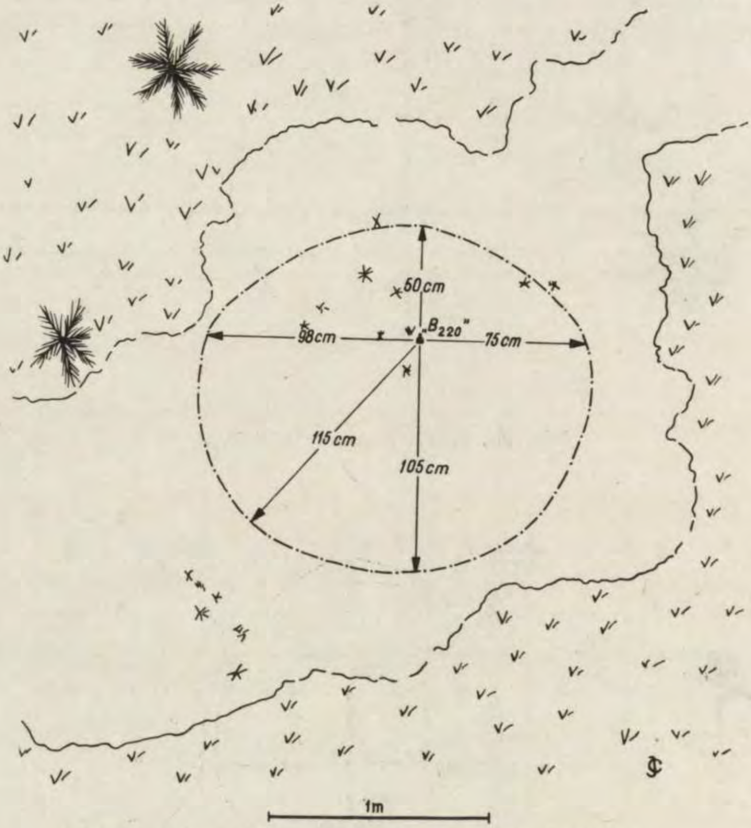

Fig. 2d. The field proximate orientation of B_{220}.

Immediate orientation

In many cases, the proximate orientation does not result in immediately finding the nest. This happens with all species whose mechanism of orientation in this stage is based on the use of orientation points or cues serving as landmarks, and not on the features of the nest itself. Under such conditions, the search for the spot at which a burrow is located, takes place with a certain degree of accuracy. This accuracy of proximate orientation, decisive for its internal limit, also determines an external limit of a tiny field for which we suggest the name of "a field of immediate orientation". It is obvious that, according to our criterion, this field can be distinguished only in the event when other means of orientation are applied by an insect within its limits or, when the behaviour of an insect in this field is essentially different.

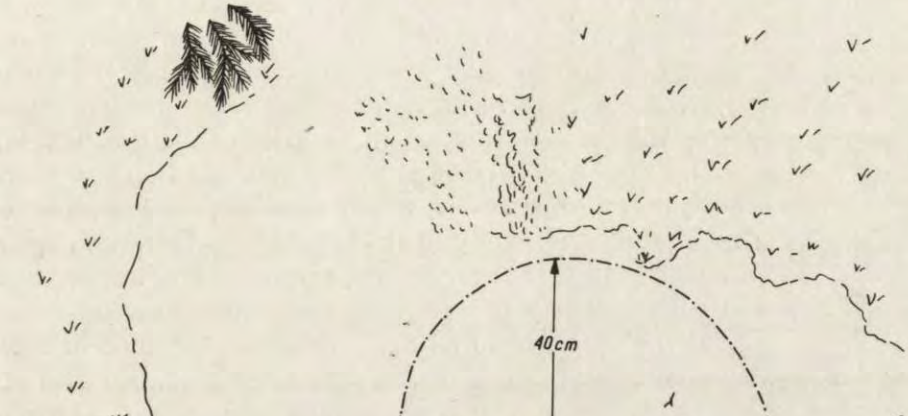

Fig. 2e. The field of proximate orientation of B_{221}, after the fairly numerous natural landmarks were removed within a radius of about 60 cm. Formerly, this field was even smaller.

The behaviour of *Bembex rostrata* (L.) does entitle us to distinguish the stage of immediate orientation because until this moment, an insect returning to its nest, covered its route flying and, now, it lands on the ground and searches for the entrance to the burrow, usually camouflaged with sand. It has been shown by the investigations that the nature of the *Bembex*' proximate orientation is visual in character (Bouvier 1900, 1901, Tinbergen 1947, van Iersel 1952, Chmurzyński 1953, 1959, 1960). In addition to sight, as believed by Marchand (1900), a certain role can, in exceptional cases, be played by smell (Chmurzyński 1959, 1960). In search for the entrance to the burrow, in the rare cases when it is still open, an insect's sight also can play a certain auxiliary role (Chmurzyński 1960), it is not, however, a fundamental sense in such a case. In his report, giving the first information on the field of the *Bembex*' immediate orientation, Molitor (1939 b) wrote that the *Bembex* found its way to the nest, that he had closed, not at once but, "she approached as if exploring the ground alternately in all directions and now and again, she dug, sometimes as far as 15 cm. sideways from the entrance to its burrow". Baerends (1941) proved that the *Ammophila pubescens* Curt., looking for the entrance to its nest, made use of touch orientation, namely, it dug only in places covered with loose sand. My own observations of the *Bembex* resulted in an identical conclusion (Chmurzyński 1960). As an example, let us quote an excerpt from a note:

> "After the *Bembex* left her nest, I levelled the surface of sand covering the burrow, which was dug in hard soil. When B_{90} returned, it flew a few very low round above the ground, hesitated for some seconds when flying over pine tree needles and small clods of earth, alighted and, feeling about with her antennas, dug into the surface of the ground. It was obvious that she tried to dig deeper in places with thick layers of loose sand."

The same result was shown in test 4. When the wasp had left its nest, it was closed by a circular or square sheet iron which subsequently was covered with a thin, about 2 mm., layer of sand. In these cases, wasps alighted on the burrow, but quickly passed along the sheet, not trying to dig much, but when they reached the edge they began to dig intensively.

This test also provides information on the extent of the field of immediate orientation. Thus, B_{230}, whose nest was covered with a 4 × 4 cm. square, at first searched within a circle 3.5 cm. in diameter; B_{228} did not leave a circle of 5.5 cm. diameter, while B_{94} — did. B_{221}, whose burrow was covered with a circle 10 cm. in diameter, landed on it and even outside it, up to 8 cm. from the burrow. However, a line encompassing an area, on which insects alight returning to their nests, should be considered a boundary of the immediate orientation field, since in the event of difficulties in finding an entrance, an insect often passes outside this boundary even as far as 20 cm. Perhaps, the distance of 15 cm., mentioned by Molitor (1939 b), belonged to this these cases.

Final remarks

In the distant orientation of female specimens of the *Bembex rostrata* (Linné 1758), a fundamental role is most probably played — in the same way as in *Ammophila* Kirby — by visual memory, recording such landmarks as, bushes, trees, roads, etc. (Baerends (1941) which also takes place in the orientation of the honeybee (von Frisch 1952, von Frisch and Lindauer 1954). The character of the flight along paths, bald patches in fields overgrown with grass, and its low ceiling, observed so many times over the 12-year period of my studies on this species, strongly speak in favour of the visual memory (Chmurzyński 1960). Of course, they do not exclude the role of the heliomenotactic orientation according to the patterns of polarization of the blue colour of the sky, as is the case with honeybees (Wolf 1926, 1927, von Frisch 1950, 1951, 1954, Lindauer 1957), which seem to be indicated by certain facts (Chmurzyński, in press a), or — the role of a muscular feeling, postulated with the regard of *Ammophila* Kirby (Ferton 1908).

This manner of orientation must exert its influence on the shape of the field of distant orientation. It is well-known that with the honeybee, it depends on the character of the terrain. In some cases, this field can stretch landwards for 13 km. from a beehive (Eckert 1933), while these insects cannot return even after short distance trips from above the open lake (Romanes 1885, Yung 1898). *Bembex rostrata* (L.) nests in sandy, open forest clearings and roads (Fabre 1879, Bouvier 1901, Vuchetich 1927, Schmiedeknecht 1930, Chmurzyński 1953). Her feeding grounds — mainly wild thyme — are also located in these biotopes. It is, therefore, highly probable that her life range does not exceed them and thus, it can be completely irregular in shape, depending on the surrounding forest (Fig. 1, within limits of open areas) and also, that the extent of this range must be influenced by the location of the *Bembex's* feeding and hunting grounds and their distances from her nest.

Since so far no experimental data are available regarding the distance of the return of *Bembex rostrata* (L.) (see Table II), I undertook preliminary experiments in this respect. Unfortunately — in view of the conditions predominating over an experimental area — all my experiments consisting in releasing *Bembeces* at a distance of more than 0.5 km. to their nests, exceeded that uniform, open biotope. In any case, under these circumstances, the longest distance of return came to 0.5 km. from the nest which, as I have already mentioned, provides us with an approximate information on the range of a limit zone of the area known

Table II

Object of investigation	Distance of return[1]	Source of data
VESPIDAE		
Eumeninae		
Odynerus (Ancistrocerus) parietinus (L.) ♀♀	200 paces — *max.*	Molitor (1937a, b, 1939 a)
Vespinae		
Polistes gallicus (L.) ♀♀	200 paces	Molitor (1936, 1937 b)
„ „ „	1 km.	Molitor (1939 a)
„ „ „ (1 young specimen)	< 100 paces	Molitor (1937 a)
Paravespula germanica (F.) ☿	< 2 km[2] – *max.*	Molitor (1937 a)
Paravespula vulgaris (L.) ☿	250 paces	Molitor (1939 a)
SPHEGIDAE		
Bembecinae		
Bembex rostrata (L.) ♀♀	(> 3 km[3] — *max.*)	Bouvier (1901)
„ „	(3—4 km.)[4]	Nielsen (1945)
Philanthinae		
Philantus triangulum (F.) ♀♀	300—400 m. — *max.*	Molitor (1934, 1937 b)
„ „	1 km. — *max.*	Tinbergen und Van Der Linde (1938)
Cerceris tuberculata (Vill.) ♀♀	3 km.	Fabre (1879)
Cerceris rybyensis (L.) ♀♀	600 paces	Molitor (1935, 1937 b)
Cerceris quadricincta (Panz.) ♀♀	a few hundred m.	Molitor (1937 b)
Cerceris arenaria (L.) ♀♀	a few hundred m.	Molitor (1937 b)
Sphecinae		
Sphex maxillosus F. ♀♀	≦ 150 m — *max.*	Molitor (1937 b)
Ammophila pubescens Curt. ♀♀	ca 80 m.[5]	Baerends (1941)
Ammophila heydeni Dahlb. ♀♀	?	Molitor (1934)
APIDAE		
Colletinae		
Colletes cunicularius (L.) ♀♀	200 m.	Malyshev (1908)
Megachilinae		
Osmia emarginata Lep. ♀♀	≤ 1 km. — *max.*	Molitor (1937 b)
Osmia spinolae Schenck[6] ♀♀	150—200 paces — *max.*	Molitor (1936, 1937 b)
Megachile argentata F. ♀♀	3 km.	Maneval (1939)
Megachile rotundata F. ♀♀	150—200 paces — *max.*	Molitor (1936, 1937 b)
Chalicodoma muraria (Retz.) ♀♀	4 km.	Fabre (1879), Molitor (1937 b)
„ „	9 km.	Fabre (1882)
Anthidium septemdentatum Lep. ♀♀	0.7 km.	Molitor (1936)
„ „	1.2 km.	Molitor (1937 b)

Object of investigation	Distance of return	Source of data
Anthophorinae		
Anthophora abrupta Say ♀♀	0.8 km. — *max.*	Rau (1929)
Tetralonia salicariae (Lep) ♀♀	800 paces	Molitor (1936)
Xylocopinae		
Xylocopa violacea (L.) ♀♀	1.2 km.	Molitor (1937b)
Xylocopa virginica (L.) ♀♀	12.5 km.	Rau (1929)
Apinae		
Apis mellifica L. ☿☿	13 km. — *max.*	Eckert (1933)
Bombinae		
Bombus lapidarius (L.) ☿☿	1.8 km. — *max.*	Molitor (1937 a, b)

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[1] Underlined and provided with the note "*max.*" are distances, over which — according to a given author — the insect could not return to its nest.

[2] The author explains that she did not return from a distance of 2 km; no positive, relative information available.

[3] A view not founded on experiments (op cit., pp. 55 — 57).

[4] A view not founded on experiments (op. cit., p. 31).

[5] A radius of a known terrain, taking in about 40 m. (op. cit., pp. 229 — 230).

[6] In original, *Osmia caementaria* (Gerst.) (cf. Dalla Torre 1896, pp. 382, 411).

to a wasp. Within these limits, I happened to find marked specimens moving spontaneously.

These limits cannot be presented in a statistical form. Although in Poland, a specimen of *Bembex* does not live in its *imago* state over a period longer than two months and these insects seem to have a good memory, phenological changes in the flora alone may cause shiftings of the extent of the life range, that is, an area known to a specimen and, therefore, also — indirectly — of a distance of return.

The field proximate orientation is dynamic to a similar extent. Its external boundary, similarly as the field of distant orientation, has the character of a zone to which the *Bembex* is led from afar by more distant landmarks, while inside it, an insect finds — *ex definitione* — the nearest surroundings of its nest, primarily by means of closely situated orientation marks. Now, as we concluded on the basis of a general character of *Bembeces*' flights, the differences in orientation features, playing an important role in these two stages, are more qualitative than quantitative in character. Hence — although we maintain that orientation and recognition flights are in principle characteristic of the stage of proximate orientation — they usually exceed that field. This happens since in the event of a disturbed orientation — and as a matter-of-fact it is precisely then that the flights discussed occur — an insect looks for points of reference to its nest and can make for more distant areas where it does not search for the nest itself.

According to my observations, such flights have the following three characteristic features. Their extent is, to a certain degree, inversely proportional to the abundance of distinct orientation marks in the neighbourhood of the nest. An insect shows a tendency to make these flights precisely in a direction aiding its orientation, that is, through an area having many environment landmarks, which are both extensive and directionally oriented such as paths, rows of plants, etc. A controversy which exists between these tendencies can be easily noticed: reaching orientation marks shortens the flight, which in turn was extended by blank spaces located between these marks. Here is an analogy to another double tendency found, e.g. that for basing the orientation, on the one hand, on terrain features situated nearer the nest and on the other, on a sufficient number of these features (Chmurzyński 1960). Now, it can be stated that the third property of orientation and recognition flights is related to it. An insect with disturbed orientation tries to extend the basis of this orientation. As noticed by van Iersel (1952, p. 391), the greater the disturbance near a burrow, the more extensive are the surroundings of a burrow used by the *Bembex* for her orientation. The individual temperament of a specimen is also important to a certain extent. Thus, for instance, after a disturbance caused by 6 blue and 6 green discs of 2.8 cm. radius being placed around the burrow, B_{52}, in its recognition flight went as far as 5 m. from the nest, while B_{181}, nesting in a quite similar place and at first annoyed only by the presence of an observer, made its flight over a field about 5 m. in diameter, but, after a disturbance was caused around its nest, flew away several times to distances of 5 to 6 m. in various directions. Of course, there can be no possible doubt as to the fact that both the flights, with a 10 m. and 5 m. radius, exceed the field of proximate orientation.

The degree of stability of the extent of this field itself is much higher than that of the zone of flights. However, its range shows analogous correlations. Thus, for instance, its extent depends on the abundance of orientation marks situated in the neighbourhood of the nest. The greater the number of natural landmarks, the more infallible is the *Bembex*' orientation and the narrower is the field of proximate orientation. This is expressively illustrated by Figs. 2 a, b in which the radius of this field nearby an orientation mark (a) is many times shorter than in open, empty terrain (b). A certain analogy can be here observed to a correlation occurring between an irregular shape of the external boundary of the field of distant orientation and topographical conditions. Furthermore, the radius of this field depends of the "intensity" (extent, quality) of durable disturbances which occurred within an environment.

Generally speaking, the length of the radius of the *Bembex*' proximate orientation field (R) could be determined as a value consisting of the maximum specific constant (C) amounting probably to about 4 m., reduced by a variable component constituting the function of the abundance of terrain in orientation marks on a given direction and their intensity (L), as well as the intensity of durable disturbances which occurred in this section of the field (D). Thus, $R \leqslant 4$ m. is in practice much less than 4 m.

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

where: R, radius of the field of proximal orientation, C, const. 4 m., L, abundance and intensity of orientation marks, D, intensity of disturbance.

This formula is of course purely empirical in character and applicable to concrete conditions of an environment. The field of proximate orientation surely depends on the structure of the field of distant orientation and cues that occur in the latter. We believe, however, that a consideration of the correctness of our scheme with a fictional field of distant orientation, deprived of any characteristic features (which would probably disturb the constancy of the component "C") is meaningless from the naturalist point of view.

A like characteristic of the proximate orientation field could possibly be carried out for other *Hymenopterons* and the constant value would be different for various species. With the bee-killer wasp, *Philanthus triangulum* (F.), the observation of this insect led Tinbergen (1932, p. 323) to estimate the radius of the proximate orientation field as 1 to 2 m. According to Baerends (1941, p. 241), *Ammophila pubescens* Curt. at first seeks its nest in an area 50 cm. in diameter, and it is only after a longer, ineffectual search that it extends this area. I, for myself, observed the search for an entrance to the nest which — after a disturbance in its neighbourhood — was undertaken by *Cerceris arenaria* (L.). ♀ at a distance of 2.10 m. from the right place.

It would seem that the field, we thus evaluated, is uniform in character. An interesting phenomenon was, however, recorded by van Iersel (1952). During his disturbance experiments, he noticed that the duration of an orientation flight is prolonged proportionally to the increase in the number of plates put near the nest, but only within a field about 18 cm. in radius. Biological analysis of this magnitude is not quite clear. The *Bembex* is not in principle classed among insects with a habit of hovering above their nests as, for instance, *Cerceris* Latr. and *Philanthus* F., and — even when it does so — it is usually at a height of about 3 cm., from which she can take in an extensive field about 3 m. in diameter. On the other hand, the acceptance of such height compels us to reject the assumption that we have to do here with a field of a two-eyed vision, since the latter is much less extensive (about 2 cm.). What could be reason bringing us to accept the idea that it is a question of a field perceived by the *Bembex* sitting near its nest? [1]

After all, it seems that this insect acquaints itself with the environment almost always during its flight (cf. Chmurzyński 1960). For the time being, this problem must remain open to discussion. It may well be, however, that within such an 18 cm. range of the environment of a nest — which could be called a *sub-range of nearest orientation*, as distinguished from an external *sub- range of proximate orientation sensu stricto* — some orientation mechanisms characteristic of it may be learned in future.

The precision of proximate orientation, that is, a field of immediate orientation, seems to have similar properties as those of the field of the previous stage of the *Bembex*' orientation, e.g., to depend on the number of clues and on disturbances near the nest. In *Aculeata* marked by an efficient spatial orientation — and the *Bembex* belongs to such — in the event of sufficiently numerous cues, that is, landmarks, this field embraces a small space. On the basis of the results of test 4, as well as observations accompanying other experiments, exceeding the scope of the present work, it may well be concluded that the magnitude of the radius of this field in the *Bembex* does not seem to exceed 3 cm. (Chmurzyński 1960). Actually, it is even smaller in practice (cf. Chmurzyński 1959), although more extensive than the field 2 cm. in diameter found by Baerends (1941, p. 261) for *Ammophila pubescens* Curt.

It is not always that the range of immediate orientation has a character of a plane surface. In *Hymenopterons* nesting on free-standing objects such as trees, and in suspended nests (honeybees, some *Vespidae* and *Sphegidae*) — it can be a spatial range. In the case of the honeybee, *Apis mellifica* L., this problem was pointed out by Bethe's (1898) and Kathariner's (1903) spectacular experiments, during which, after shifting a beehive only 50 cm., many honeybees, returning from the field, crowded in the air exactly where the beehive entrance was located before. The same phenomenon was recorded by Rabaud (1926) in the case of the vertical change in the position of the entrance to the nest

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[1] On the assumption that the vision angle of the ground equals 89°, the range of vision of 18 cm. to each side yields a theoretical height of 3.2 mm. (cf. Chmurzyński, in press b).

of the wasp, *Dolichovespula silvestris* (Scop.), which was shifted only 50 cm. and, by Malyshev (1908) with the *Osmia rufa* (L.), when the tube of its nest was pushed forward by a mere 2 cm. It seems, however, that insects that nest in the soil do not possess such stereometric orientation capabilities, because — when the entrance to the corridor of *Halictus sp.* was lifted by Malyshev (1908) by 20 cm. — the mining bee found a new entrance at once. Probably, the case of the *Bembex* is somewhat similar.

On the basis of Rabaud's (1920) experiments with *Polistes gallicus* (L.) and *Dolichevespula silvestris* (Scop.), as well as by Verlaine (1925) with *Paravespula germanica* (F.), a conclusion might be drawn that the finding of a nest by the wasp is still not synonymous with positive identification as its own nest. Information regarding this fact is given largely by an insect's sense of smell, as well as by the elements of the internal architecture of the nest, which are perhaps recognized by means of touch and kinaesthesia.

Some light is thrown on the problem of Hymenopterons' orientation inside the nest by maze experiments. Kalmus (1937) proved that the honeybee masters the situation inside a dark maze quite well, where it is helped to a considerable extent by its antennal sense. Similar problems, with particular consideration of training wasps of the genus *Paravespula* Blüth. and honeybees inside a maze, were studied by Weiss (1953 and subsequent papers) in his series of experiments. A remarkable and interesting phenomenon was observed insofar that insects — in the same manner as in vertebrates — learn to know their way "back" and "forth" quite independently. An interesting monograph, dealing with the behavior of the Japanese digger wasp *Bembex niponica* Smith, has been worked out by Tsuneki (1956—1958).

The experimental investigation of these stages of the *Bembex rostrata's* (L.) spatial orientation still remains an open question.

SUMMARY

The aim of the present paper is to evaluate the character of the return of the *Bembex rostrata's* (L.) female specimens to their nest, examined from the point of view of stages into which the spatial orientation of these insects might be divided.

On the basis of the attempts to divide a return flight into stages, undertaken thus far, an extended Rabaud's scheme is presented by the author, who subsequently concerns himself with the first three stages: 1) finding the site of the nest, that is — distant orientation, 2)

recognition of the closest surroundings of the nest — proximate orientation, and 3) finding the entrance to the nest itself — immediate orientation.

In contradistinction to animals with astronavigational orientation, the *Bembex*, an insect with typically visual and topographical orientation, has a limited field of distant orientation, which perhaps slightly exceeds a territory known to it, that is, the so-called "life range". A radius of this field, which in practice is never circular in shape, depends on many ecological factors such as, the shape of a biotope peculiar to the *Bembex*, the location of hunting and feeding grounds, etc. For practical reasons, only the distance was examined, from beyond which first marked insect ceased to returned. It amounted to 0.5 km. One possibility should be reckoned with, that the life range can sometimes exceed this limit, not to mention the boundary of the field of distant orientation in the sense of the furthest distance from which insects are able to return to their nests.

Despite the appearances, resulting from the similarity of the flight of the *Bembeces* near and far from their nests, the orientation in the neighbourhood of a nest constitutes in this insect a separate stage. In the light of (1) the observation of recognition and orientation flights, as well as of (2) abortive digging by insects with strongly disturbed orientation, the field of proximate orientation stands clearly separated from the field of distant orientation. The best estimate of its extent is given by (3) "test of a shift" in which a wasp — as a result of shifting its training system — is compelled to dig far from its real nest. These three paths of experiments yield a relatively concurrent result: the proximate orientation extends, on the average, about 4 m. from the burrow and the number of landmarks in a given direction from the burrow causes a lessening of this radius, which in turn is counteracted by the disturbance in the neighbourhood of the nest, so that in practice, this field is — as the previous one — irregular in shape.

There seems to be a supposition, founded on a phenomenon recorded by van Iersel (1952) that — within the field of proximate orientation *sensu lato* — two concentrical sub-stages exist in the *Bembex*, that is, a sub-stage of proximate orientation *sensu stricto* and a sub-stage of nearest orientation, the latter with a radius of about 18 cm. No indications as to the differences between the mechanisms of orientation in these two sub-stages are available thus far.

When in the vicinity of its burrow, the *Bembex* is put in the right way by orientation points or, landmarks which lead this insect to a tiny field of immediate orientation, usually not more than 3 cm. in radius, from which it looks for the entrance to the nest itself. This takes place by using its sense of touch, aided by sight.

Certain suppositions were also brought forward concerning the recognition of the nest itself and the orientation inside it.

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