ON THE FUNCTIONAL ORGANISATION OF DRIVES*

BY ERICH v. HOLST AND URSULA v. SAINT PAUL

in memory of our good friend GUSTAV KRAMER (killed 19th April, 1959)

(Translation by J. E. Burchard jnr., of a paper which appeared originally under the title *Vom Wirkungsgefüge der Triebe* in *Naturwissenschaften*, **18**, 409-422).

Introduction: The Problem of Localization

The human mind always wants to order its environment. Each thing which differs from others in its application, mode of functioning, and appearance receives its own place and name. This way of thinking has also proved itself in the study of vital processes, which in fact do take place in organs, differing from each other in performance, mode of operation, appearance, and position. Only in the case of the central nervous system (CNS) does this anthropomorphic will to order fail. The achievements of this entity are exceedingly varied. To name only a few: retaining a particular temperature value as reference point for temperature regulation; reflex movements as a protection against damage from outside agencies; preservation of an extract of past sensory data for use later on; carrying out various seeking activities, corresponding to changing bodily requirements: adaptation of the visual process to different light intensities so as to ensure good perception of objects; "filtering out" particular stimulus properties of the outer world, to which appropriate instinctive behaviour patterns can then be linked up. If the interior of a part of the body with so manifold capacities were only now to become accessible to investigation for the first time, we should expect to find there a large number of different organs. As is well known, in the CNS—unfortunately—the opposite is the case; we find no recognizable organ boundaries, but everywhere almost identical structural elements, the neurons, in staggering numbers.

This morphological state of affairs has continually tempted investigators to search for "the" functional principle of the CNS. Thanks to its manifold capacities, moreover, this organ system is able to answer the most diverse experimental "leading questions" with a conciliatory "yes"—even to postulates which are mutually exclusive. In this way have arisen the extreme forms of the reflex doctrine, of the doctrine of the "conditioned" reflex, the thesis that all actions are learned, the doctrine of centres and the doctrine of plasticity, as monistic exaggerations of partial truths.

For many investigators, now as in earlier times, the most important question concerns the place at which a function occurs, the *localization problem.* The *doctrine of centres* finds abundant evidence for an anthropomorphic order: the elimination of certain functions by local brain damage is proof of organization into centres with afferent and efferent pathways. The *doctrine of plasticity* provides abundant examples of just the opposite: the impossibility of finding a specific area, for instance for memory or for the co-ordination of movement. The doctrine of centres argues further: if local electrical stimulation elicits particular reactions, then centres can be "functionally" defined in this way. The opponents of this view reply that afferent or intra-central pathways would then, grotesquely enough, become "centres" at whatever point the electrode happened to strike them; for it is just such pathways which most easily initiate responses. Only slowly has the contest between these arguments led to abandonment of the anthropomorphic scheme of organization. One may think that it might be economical to distribute the neurons serving a given function over a wide area, and to intersperse them with those serving other functions—namely, when cross-relationships among these functions are called for.

The most rigorous attempt to clarify the localization problem for a particular region of the brain is due to W. R. Hess (1954), who, by stimulating with implanted electrodes and marking the stimulated points by electrocoagulation, created in the course of many years a histological atlas of the midbrain of the cat, with many stimulus points for various reactions. The result brings no decision in favour of either of the two doctrines: many reactions could be elicited over a wide area, though always from specific places, between which sites for other reactions occurred; yet there were also brain regions for only a few functionally interrelated actions.

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*Progress report on a four-year collective programme with E. Baeumer, W. Jechorek, Renate Hübbe and R. Jahde. The contents of this paper were presented in expanded form at the International Ethological Conference in Cambridge, September, 1959.

Programme and Methods

Our own experiences with the internal dynamics of the CNS (v. Holst, 1939, 1956) and tentative experiments with a stimulation method derived from that of Hess have led us onto another methodological path. They confirmed a long-standing suspicion that the investigation of the physiological questions "How?" and "Why?" is usually deflected much too soon into the morphological question "Where?" (v. Holst, 1937). Thus the histologist is burdened with problems which only the physiologist can solve, by delving deeper into the central dynamics. We have therefore formed two distinct research teams, one of which studies only the central functional organization, the *Wirkungsgefüge*,[*] while the other studies the histological structure.[†] Not until the physiological method is confronted with insurmountable obstacles do we plan to attempt to correlate the functional with the histological organization.

Our experimental object is the domestic fowl, with its wealth of gestures and calls, its drastic sexual dimorphism, and its social structure. As to method, let is suffice to say that insulated silver wires, 0, 12 mm. in diameter and with uninsulated tips 0·3 to 0·5 mm. long, are pushed into the brain in calibrated steps by means of a small screw arrangement made fast to the skull. Of the four (sometimes eight) electrodes, some are always left as indifferent electrodes in the "silent" roof of the brain, while the remainder are used to seek effective fields of stimulation in the depths (Plate I); it is impossible to say how large or of what form these fields may be, since the CNS is a *non-homogeneous* conducting mass. It cannot be taken for granted, furthermore, that the structures excited always lie in the immediate proximity of the electrode tip; when for example the tissues surrounding the electrode are destroyed by electrocoagulation for a distance of 0·3 to 0·5 mm., the previous reaction may still be present when stimulation is renewed.

The intact and unrestrained animals—which can be used again and again for years without the slightest ill effect—are free to move about a table).[‡] From the brain region indicated Plate II nearly all known movements can elicited, serving orientation and the needs of body, directed towards enemies, rivals, the partner and the young, with all the associat calls.[§]

Grounds for Confidence and Lack of Confide in Localization

Fig. 1 shows examples of how, when sti lating with sinusoidal alternating current, threshold voltage at which the reaction beg depends on the frequency. The threshold ha minimum at 50 to 100 cycles per second, a climbs steeply with decreasing frequency, l steeply with rising frequency. One could th

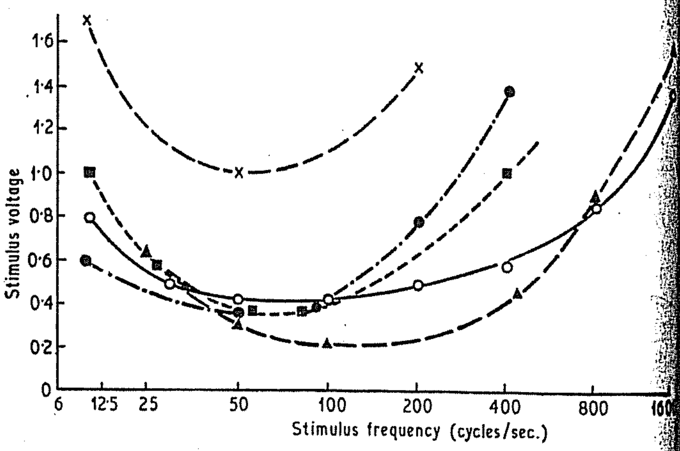

Fig. 1. Examples of the dependence of the necessary stimulus vol (threshold voltage) on the stimulus frequency. (Sinusoidal alterna current; Reactions: x and ▲ clucking, ● looking about (Aufmerk with jerky head movements in all directions, o calling to fo ■ watching out (Sichern) with extended neck and motionless head)

using a constant high voltage, ascend from cycles or descend from 2000 cycles, and measu the threshold in cycles; or on the other hand as we have done—express the threshold in vo at a constant frequency of 50 cycles.

Let us trace, with such threshold measu ments, the path of an electrode as it penetra in tiny steps downwards somewhere in the bra stem. One should expect that as it passes by

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[*] The expression "Wirkungsgefüge" (control pattern or functional organization—Gefüge=structure, system; Wirkung=effect, operation) was proposed by H. Mittelstaedt (1954); we had previously spoken of "functional structure" (Funktionsstruktur) (1939).

[†] Under the leadership of W. Hirschberger.

[‡] A method of wireless stimulation has also been develo (Jechorek & v. Holst, 1956) but will not be discus here.

[§] A film showing the method used, and several fi showing most of the reactions obtained as well as so experiments discussed later on, have been publis by the Institut für den Wissenschaftlichen Film Göttingen).

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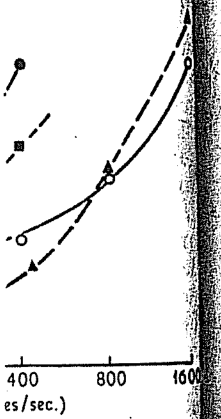

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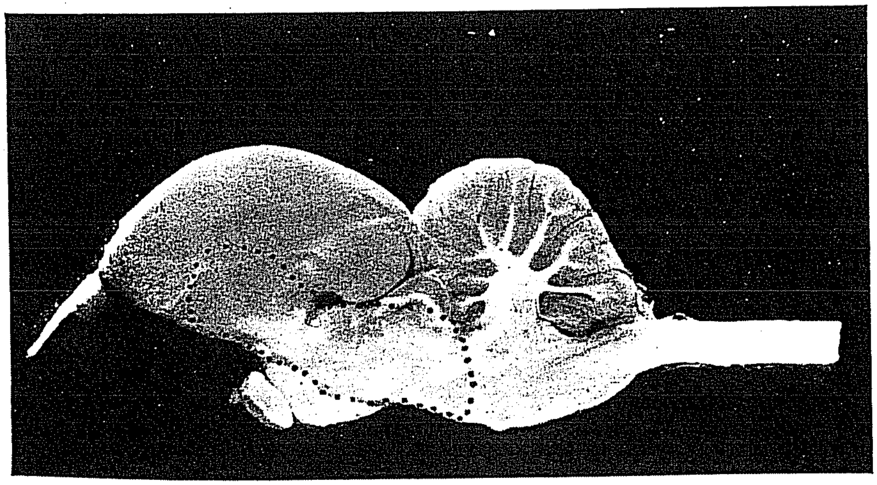
PLATE I

Radiograph of a hen's head from the side, in which are implanted two brain electrodes. The small dark square beside the ends of the wires and the triangle above right mark the auditory passages, the upper quadrangle between the four electrodes marks the end of the (invisible) Plexiglas electrode holder, which is screwed to the roof of the skull. Important areas of stimulation can be roughly localized with the aid of such pictures taken in two directions.

PLATE II



Longitudinal section of the brain of a fowl. The areas of stimulation explored lie in the region of the brain-stem marked with a dotted line.

PLATE III

Cock showing 'wing-scratching' as a consequence of brain-stem stimulation (0·15 volts). This is a display in which the animal circles a subordinate companion, usually a hen, scratching with the outer foot at the down-stretched outer wing. Here, in the absence of another fowl, it is a 'vacuum-activity'.

localized excitable structure the threshold value would be high at first, then low at the point of closest approach, and then high again. This is, in fact, often the case; Figs. 2 and 3 give examples. In many other cases the threshold curve is irregular and extends over as much as several millimetres (Fig. 2, bottom, ● □), which perhaps means that the electrode is travelling parallel to a fibre tract. When the stimulus voltage is increased, other reactions usually appear in addition to (or instead of) the first (Fig. 2, bottom); this too is understandable, since the region of adequate stimulation has expanded to affect new structures.

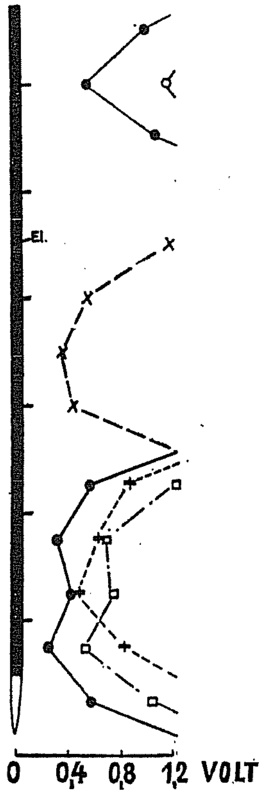


Fig. 2. Examples of the appearance and disappearance of reactions as the electrode (El.), is pushed forward in the brain stem. The horizontal markings along the electrode path designate millimetre intervals. The horizontal distance of the points from the electrode indicates the threshold voltage (see scale below). The reactions are: ● looking out (Aufmerken); × watching out (Sichern); + head-shaking; ○ turning to the left, □ turning to the right.

Less illuminating is the common situation, that the same reaction can be obtained from various fields of stimulation; in the intervening area, other behaviour patterns are elicited (Fig. 2, ●). This fact, well known in the literature, is difficult for the histologist to interpret; we shall see, however, that it has a physiological explanation. Completely mystifying for the histologist, finally, is the common phenomenon that the electrode, moving for a second time along the same path, produces different behaviour, even with the same stimulus strength. A relatively innocuous example of this is shown in Fig. 5, where at one location a turning movement appears in place of looking around (Aufmerken). If one leaves the electrode in one spot and extends the experiment over several hours, it is not unusual to obtain at times nothing, then perhaps running away a couple of times, later on clucking, after that fluffing out of the feathers, and finally perhaps preening—all from the same field with the same stimulus voltage. This blow to the proponents of localization, too, follows from rules of the functional organisation, which we shall come to know,

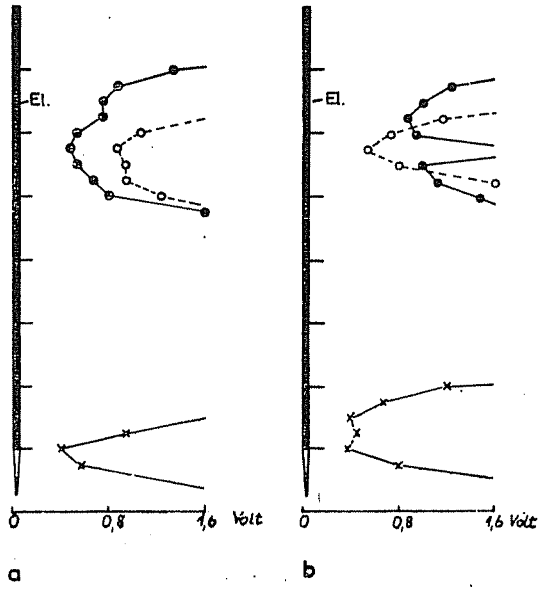


Fig. 3. Another example of the appearance of different behaviour patterns as the electrode moves deeper; details as in Fig. 2. ● looking about (Aufmerken), ○; turning to the left, × fleeing downwards; in *a* the electrode was moved downwards, in *b*, about 30 minutes later, it was withdrawn upwards along the same path.

Precision of the Method; the Compensation Formula; Measurement of Visible and Invisible Phenomena

The behaviour of a higher organism is the result of a complicated interaction of qualitative and quantitative data; is the method at all accurate enough for the task of measuring these data? The facts just mentioned encourage scepticism.

Many things might be quantified: the necessary threshold voltage, the latency with which the reaction follows the beginning of stimulation, the intensity of the reaction (i.e. speed or amplitude of a movement, volume of a sound), the frequency in cases of rhythmic response, and finally the duration of the reaction—always with the condition that the *quality* of the behaviour remains *constant* throughout the series of measurements.

Let us look at some examples to confirm the regularity of the phenomena. For movements with a well-defined beginning, a good quantity to measure is the *latency*, whose relationship to the *stimulus voltage* is shown in Fig. 4 for the example of the aerial-warning cry. Here, as in other cases, the values lie — other things being equal—on a hyperbola-like curve; as the voltag rises, the necessary stimulus duration sinks. Th product of these two quantities would be constant in a hyperbola; here, however, it is constant over a wide range only if we first subtrac a certain amount—about two thirds of the lowest threshold voltage, the "Rheobase"—as shown for three such experiments in Fig. 5. Only with very high stimulus voltages, at the left-hand end of the curve, is there a downward bend here the product becomes smaller, which is to sa the stimulation is more effective.

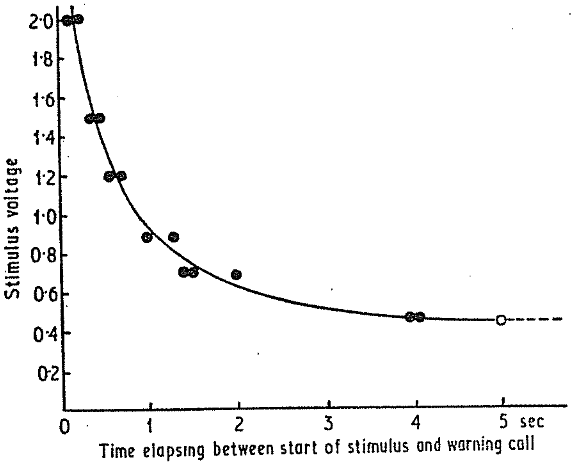


Fig. 4. Dependence of the latency on the stimulus voltage for the aerial-warning call ("Klock") of a cock. Here and in all further measurements, sinusoidal alternating current of 50 cycles/sec. has been used. (The stimulus voltages were varied at random in the experimental sequence; the first stimulus which released no reaction is indicated by ○).

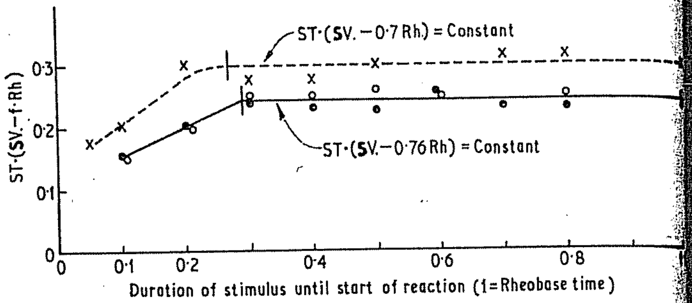


Fig. 5. For three experiments of the type shown in Fig. 4, the product o the stimulus time (ST) times the corresponding stimulus voltage (SV minus a part of the lowest effective stimulus voltage, the Rheobas (f·Rh), is plotted as a function of the stimulus duration (× aeria warning call of the cock, ● headshaking, ○ "alert call" (Wachlaut), a brief explosive burst of cackling).

It seems as if we might here be dealing with rather general law; this cannot be tested accur ately with the latency method, however, in case where the behaviour begins gradually, for in stance sitting down or turning the head to on side. Here a methodological trick is useful: th behaviour patterns activated in the brain ste continue smoothly if the stimulating current rhythmically interrupted (between 4 and 1 cycles/sec.). It is then possible, using a consta interruption frequency, to vary the length o the stimulus pauses and measure the corre ponding rheobases, that is the minimum voltag necessary to produce any reaction at all. The values are correlated with the ratio of stimulu length to pause length and are independent o the latency; the latter disappears from th equation. Fig. 6 shows nine series of exper ments conducted in this way; all the curves a quite similar. When they are reduced to the sam initial value, averaged, and plotted similarly t Fig. 5, the curve shown in Fig. 7 results; it is full agreement with the results of the latenc

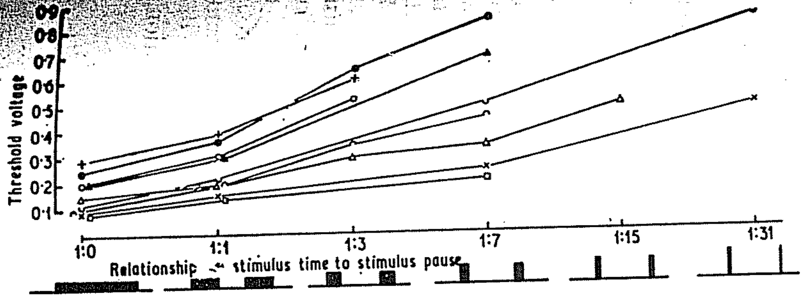


Fig. 6. Measurement of the threshold voltage for continuous stimulation (alternating current, 50 cy/sec.) and for rhythmically interrupted stimulation with increasing length of pauses and decreasing length of stimuli, as the sketch below suggests. (× headshaking, ▲ turning head away, ○ sitting down, the other 6 symbols indicate clucking). The frequency of stimulus interruption, between 4 and 10 cycles per second, is without effect.

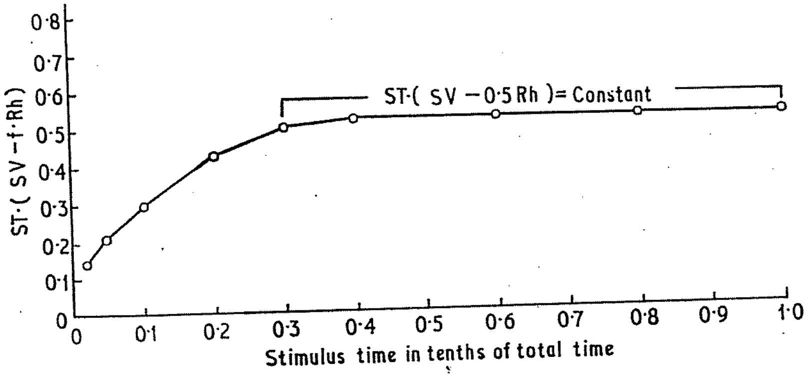


Fig. 7. The values of Fig. 6 are summarized, recalculated as in Fig. 5 according to the formula: ST·(SV—f·Rh), and plotted as a function of the ratio of stimulus time to total time (thus 1 is continuous stimulation, 0·5 indicates that stimulus time equal pause time, and so on).

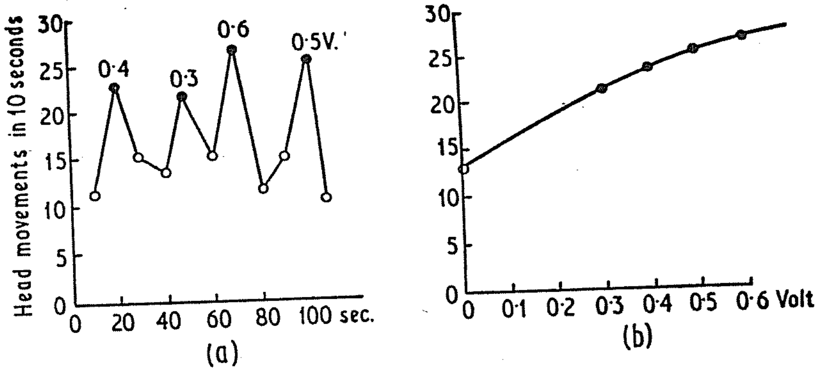


Fig. 8. Spontaneous jerky head movements in all directions—looking about (Aufmerken)—are increased by stimulation. *a* shows the frequency increase of the head jerks in the sequence of the experiment; *b* the same in systematic arrangement. The figure does not show that during stimulation the head jerks are directed forward and merge into intention movements of picking at little particles on the ground or on the bird's own body. (○ spontaneous frequency, ● frequency during stimulation).

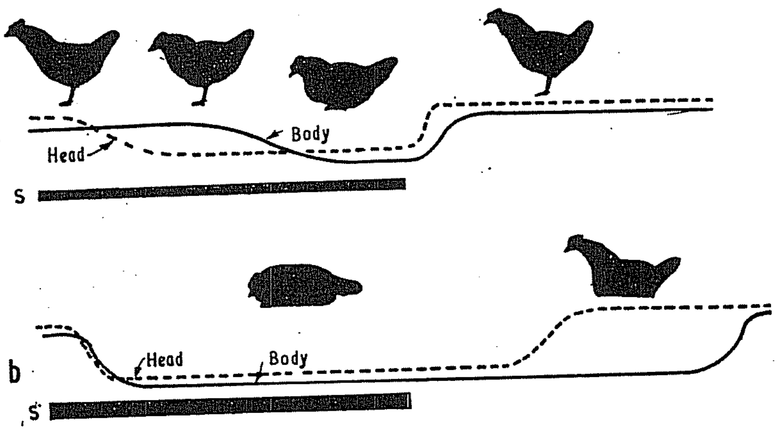


Fig. 9. Effect of two sitting stimuli of different strengths on a quietly standing fowl; pulling in the head and lowering the body are registered separately; the stimulus (S) amounts to 0·5 volt in *a*, 0·7 volt in *b*. (From cine film).

measurement as shown in Fig. 5. We have thus found a general formula describing the way in which the intensity and the duration of the stimulation substitute for one another, or compensate each other: the *compensation formula*.

The measurements thus far have used thresholds of behaviour; these thresholds vanish when the stimulus-dependent activity is already present spontaneously, as Fig. 8 shows for the jerky head movements in looking around (Aufmerken). Here the frequency gives a good measure with(other things being equal) reproducible data; one can see that the curve tends toward a "saturation" value of about three movements per second.

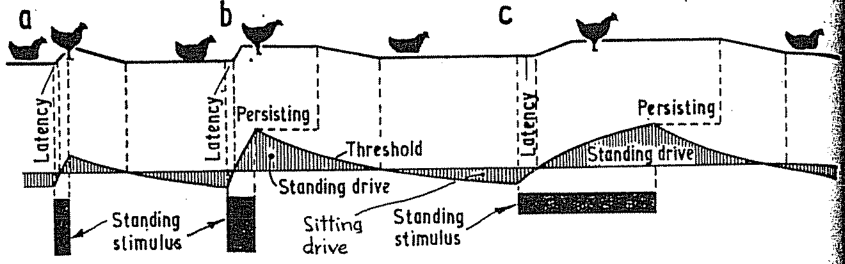


Fig. 10. Sketch to illustrate the interrelation of various parameters of the behaviour. Explanation in the text.

Fig. 9 shows, finally, with sitting down as example, the dependence on the stimulus voltage of four different quantities: latency, speed, amplitude, and duration of the movement. We shall consider for the moment only the striking phenomenon of *after-response*, here dependent on the stimulus strength (and thus, according to the compensation formula, also on the stimulus duration) (Fig. 9b). What is the immediate cause of this rather common continuation of the activity long after the end of stimulation? Has the stimulus piled up some specific something centrally, which is slowly "used up", and can this invisible something be measured?

The student of behaviour knows that actions which are externally the same can be internally of very different intensity. A sitting hen can be slightly or strongly "inclined to sit"; in the first case she can be distracted easily by other stimuli, in the second case with difficulty. The same is true of so many activities, the degree of whose necessity or "drive" is not outwardly apparent, such as standing, drinking, sleeping, preening, picking off of vermin, crowing, etc.* One can, however, always measure this "drive" by means of a second stimulator and a second electrode, with which one seeks out the stimulus field of an opposing response. To make clear the principle, the simple scheme of Fig. 10 suffices, in which sitting down and standing up were played off against one another: at the same time this scheme brings all the quantities so far discussed into a natural relationship.

The subject is a hen with spontaneous "sitting drive", which we cause to stand up by stimulation of a central "standing field". The first stimulus (Fig. 10a) is strong but short; the animal stands up quickly after a brief latency, and sits down again at once. The second stimulus (Fig. 10b) is strong and longer; latency and standing up are unchanged, but the standing persists for a time after the end of stimulation. The third stimulus (Fig. 10c) is weaker and much longer; the latency, following the compensation formula, is longer, the hen stands up slowly, and the standing persists, again following the compensation formula, just as long after the end of stimulation as in the second case. As common cause of these experimental facts central process may be postulated, indicated by the curve running across the middle of the figure; it has the value zero at the point where sitting changes to standing; below the zero line we call it physiological *sitting drive*, above the line *standing drive*. This postulated central process is, in fact, directly measurable: as long as the animal is sitting, the threshold voltage for standing up gives a measure of the sitting drive that must be overcome; as long as it is standing, on the other hand, the threshold voltage which must be applied at any particular moment to central "sitting field", in order to induce sitting down, is a measure of the standing drive. The schematic course of the whole threshold curve is drawn according to such measurements using two complementary stimulation fields. It defines, first of all, the magnitude and direction of the central drive—whose physical nature is of course completely obscure—; secondly, it determines in a readily apparent way the visible data: latency, speed, duration, and their relation

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*In order to make more data visible, we have sometimes also recorded respiration and heartbeat; nothing further will be said here of these, nor of the changes in action potentials which can be recorded from the electrodes during the pauses in stimulation.

stimulus strength and duration. And in so doing, thirdly, it explains the principle of the compensation formula.

An Excursion on the Precision of the Method

The previous chapter has made clear that the method can satisfy high requirements as to exactness and reproducibility. But under what conditions? what, for example, does the frequently cited qualification "other things being equal" mean? The answer is this: the method is exact only so long as the *internal* central situation remains constant, in which every action is, as it were, imbedded. Many and various factors, temporally often far removed, influence this situation; we shall become familiar with the most important.

How does one attain a constant—or at least known—*internal* situation? It is no use grabbing an animal from the henhouse, inserting electrodes (under anaesthetic), and then, when it wakes up, beginning the stimulation experiment: most of the stimulation fields remain silent, while from others one gets mainly "freezing" and various sorts of fleeing: reproducible curves are unthinkable. If one succeeds, in the course of hours, in getting the animal to settle down somewhat, many of the silent regions will become active, and fleeing will become confined to fewer stimulation fields; if one is fortunate enough to "put over" perhaps a brooding, sleeping, or crowing reaction, the ice is generally broken for the time being. Precondition for all measurements is a calm, "comfortable" basic mood, in the fowl very roughly characterized by loosely lying plumage, alert looking around, tendency to preen, to eat, to sit down, and in the cock also by spontaneous crowing, by watching out ("Sichern") and (perhaps warning), and by calling to food. Even the slightest tension (tonic immobility or "freezing") can ruin everything. To be able to differentiate such fine nuances in posture and movement, a knowledge of the full inventory of behaviour is just as essential *before* beginning the experiments, as it is afterwards necessary for the correct identification of every reaction.* Once the desired neutral basic mood has been approximated, one obtains, in the course of the next few hours, as more stimulus fields are reached, correspondingly more and more control of the whole situation, and is then in a position to measure factors which *change* this internal situation; we will now direct our attention to these.

Central Adaptation and Mood Shifts (Umstimmung)

To the observer of animals it is a familiar story, that a stimulus situation sets a particular action going with at first rapidly rising and then gradually declining intensity, as if at first an "initial friction" had to be overcome, and as if the behaviour later became "fatigued". This phenomenon also appears quite generally when a field in the brain is stimulated (Fig. 11a). If one measures it in terms of stimulus thresholds, the threshold starts out high, then falls rapidly, and later climbs slowly up again (Fig. 11b).

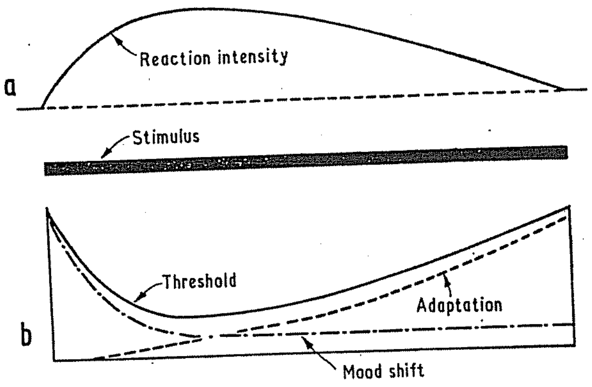

Fig. 11. *a*. curve illustrating the rise and fall of a reaction with constant stimulation. *b*. Initial decline and subsequent recovery of the threshold, for the same reaction as in *a*. The way in which this threshold curve results from two processes, the one increasing and the other decreasing, is explained in the following text.

We will first examine the "fatigue" phenomenon. Fig. 12 shows the fading away to nothing of a clucking reaction, in twelve successive identical stimulation series; one can see here how the shortening of the response duration comes about through rising latency and symmetrically corresponding decline in after-response. In the experiment shown in Fig. 13, the same clucking is a component of a more complex fleeing behaviour. Here, following the scheme of Fig. 11b, the stimulus was increased parallel to the slowly rising threshold; thus not the stimulus strength, but the reaction was held constant. Here it is abruptly ended by the appearance of a new behaviour element, flying away.

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* We wish to thank our co-worker, the outstanding fowl specialist Dr. Erich Baeumer, for introducing us to the very extensive catalogue of fowl behaviour; in all doubtful cases, we have relied on his cautious interpretation.

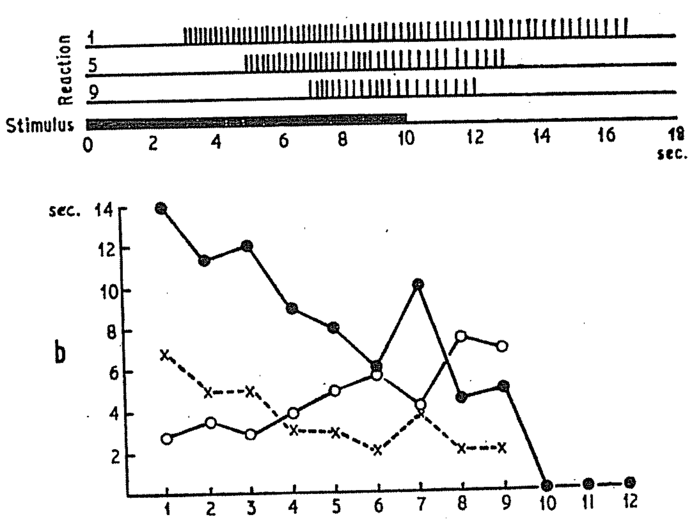

Fig. 12. A stimulus field for clucking was "pumped dry" by a series of 12 stimulations, each of 10 seconds duration (with intervals of 10 seconds between stimulations). *a* indicates the result of the first, fifth, and ninth stimulations; *b* gives for the 12 stimuli the latencies (o), the persistence (x) or after-response duration, and the duration of the response (●).

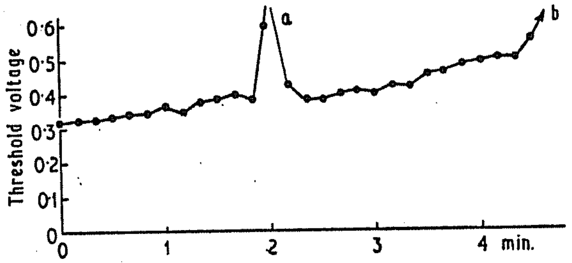

Fig. 13. A fowl is brought into fleeing restlessness through stimulation (the behaviour elements which appear are shown in Fig. 25a). The continuous stimulation was gradually increased in such a way that the animal was constantly clucking softly; the stimulus voltage was read off every 10 seconds. At *a* the bird defecated, at *b* it flew off with a brief screech.

All such cases of decrease in reaction (or of increase in threshold) have one thing in common: they give the same picture as would be given—other things being equal—by a decrease in *stimulus voltage*. One might suppose that the conduction path from the stimulus field to the neuromotor apparatus proper is being increasingly blocked at some point or other.

In favourable cases it can, in fact, be shown that this suspicion is correct. For a simple and common reaction, for example clucking, we search out two different, widely separated stimulation fields. With two ind
pendent stimulators we can now ca
out a variety of stimulus combinatio
(Fig. 14), from which many kinds
information can be obtained. We ca
for example, apply to each field
voltage, which produces a modera
reaction; then both fields are stim
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pears, as expected, an increased
action (Fig. 14b). There is thus
doubt that the two excitations flo
together and are summated *somewh*
in the CNS. Now we stimulate o
field alone for a longer time, un
after the behaviour has faded o
and then at once stimulate the oth
field alone; the reaction immediate
reappears in full force, and vice ve
(Fig. 14c). First of all, this confir
that we are dealing with two disti
physically non-overlapping fields
stimulation; and it further sho
that the fading out takes pla
before the two excitations flow together, si
otherwise the effect would necessarily still
noticeable in the *other* stimulation field.
follows, then, that less and less excitation do
in fact get through to the neuromotor apparatu
We therefore designate the phenomenon
central, local *adaptation*.

If this is all true, it has still another con
quence: when a field is continuously stimulat
this afferent structure should *remain* conti
ously adapted, so that the extinguished beha
iour does not reappear no matter how lo
stimulation is continued. This is, in fact, reg
larly the case, and expresses itself particula
drastically for reactions which adapt very quic
so that stimulation results in but a single "d
charge", for instance crowing, the aerial-warni
cry, the "Alert call" or "Wachlaut" (a br
"burst" of cackling). Thus, it is not unus
for a cock to crow but once with continu
stimulation of a particular "crowing field",
if the stimulation is briefly interrupted af
each call, it may crow 20 times or more wit
5 minutes! This shows very nicely that a "f
igue" of the neuromotor apparatus itself is o
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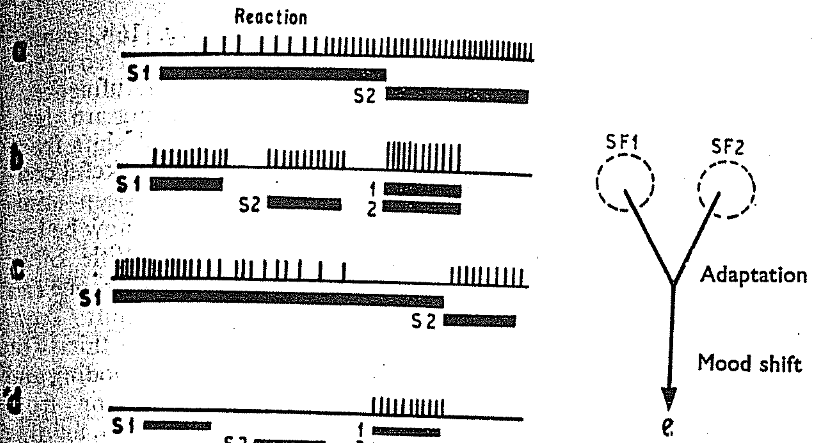

Fig. 14. Scheme to explain various combinations in the stimulation of two fields for the same behaviour. Based on a case in which the two stimulation fields lay in the right and left brainstem halves, laterally separated by a distance of about 5 mm., and gave "pure" clucking. To be certain of excluding a possible mutual physical interaction due to voltages produced in the tissue by the two pairs of electrodes, when both fields were stimulated simultaneously, rhythmically interrupted stimulation was used (as in Fig. 6) in such a way that when both fields were stimulated the stimulation in one fell during the pauses in the other. (S stimulus, SF stimulus field; further explanation in the text).

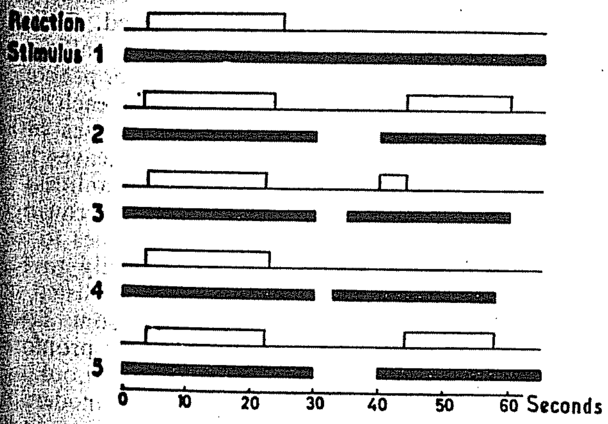

Fig. 15. Dependence of a reaction—cleaning tongue movements in the mouth—on the stimulus duration and stimulus pause. The stimulus voltage is constant (0·5 volt). With prolonged stimulation the reaction stops after about 20 seconds, and the occurrence and duration of its reappearance depend on the length of the pause in stimulation.

follow the process of *de*adaptation; in the experiment in Fig. 15 it required something more than 10 seconds.

These data once again show that it is possible to measure something that is not directly visible; here it is not a drive, but a localised process in a conducting structure. The existence of such *subthreshold* events is, as we shall see, important for the localization problem; it can be demonstrated still more directly in the experiment with two stimulus fields for the same reaction. In many cases, namely, when both fields are stimulated simultaneously by voltages each of which alone is wholly ineffective, a clear reaction occurs (Fig. 14d). This means, however, that both "subthreshold" excitation processes must be transmitted at least as far as the place where they come together, since otherwise they could not summate and so raise the behaviour itself over the threshold. Thus the threshold, which must here be overcome, does not lie in the stimulation field at all, but *somewhere* on the way to the motor apparatus.

Now let us consider the other phenomenon: the decline of the threshold at the beginning of a long-continuing or frequently repeated action. (cf. Fig. 11b). As Fig. 16a shows, this effect can be absent entirely, when the stimulus is infrequent (or short); the threshold curve remains on one level. The more closely the stimuli follow one another, the more steeply does the threshold curve fall—here even to zero (Fig. 16c); that is, the *re*action becomes a *spontaneous* action. In other cases, the latency can serve as measure instead of the threshold (according to the compensation formula); here too, tremendous initial changes can appear, for which Fig. 17 gives an example.

In surveying numerous similar cases, it will become clear to the observer that the curves only show *one* side of the situation, for every such decline in threshold is accompanied by a simultaneous rise in the thresholds for certain other activities. We are dealing with the displacement of an equilibrium condition, along the lines indicated in Fig. 10, except that here much slower processes are involved, which are overlain by the threshold relationships of the activity itself, without necessarily being influenced by them. Thus for instance in Fig. 18 a long sustained scolding mood is interrupted from two stimulation fields. One of the stimuli—watchful staring (Sichern)—has only a slight

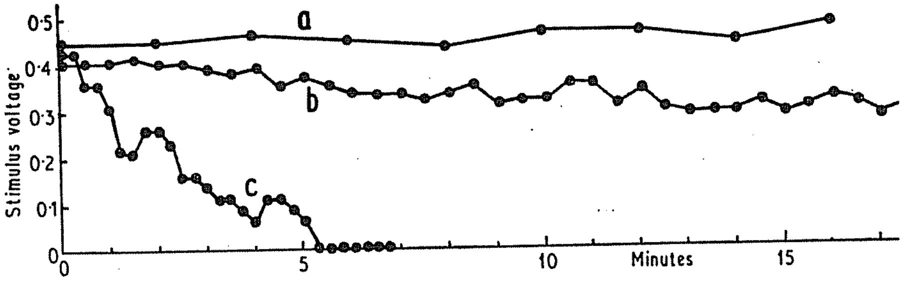

Fig. 16. A fowl sits motionless (sleepy) in dim light. A field is stimulated which produces looking about (Aufmerken), with a stimulus which increases (by 0·1 volt every 3 seconds) until the first head movement; then the stimulus stops instantly. In *a* stimulation was every 90 seconds, in *b* every 30 seconds, in *c* every 15 seconds.

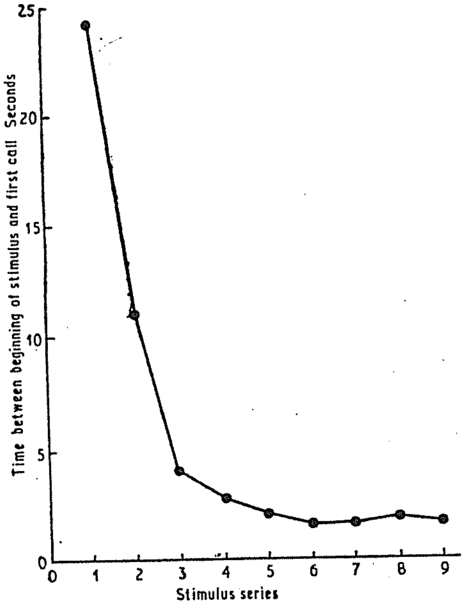

Fig. 17. A quietly sitting fowl was repeatedly stimulated with a constant stimulus (0·4 volt) in a field for clucking, each time until the first cluck; the stimulus duration (latency) was measured. Between one stimulus and the next was a pause of 5 seconds (only the first two stimuli, not shown here, had other voltages; 0·38 volt: no reaction; 0·42 volt: reaction after 3 seconds).

influence, the other—sitting down in sleepy mood—is more effective; with brief stimulation, nevertheless, the scolding mood is not yet altered. After a prolonged sitting stimulus, however (Fig. 18b) the hen stands up and is quite pacified. One sees, as in Fig. 16a, that the basic mood has an inertia and requires time to change. We designate such gradual changes of a basic tendency as *mood shifts*.

In Fig. 16b, c an Fig. 17, lookin around (Aufmerken and clucking are sig of a mood shift fro sleep to a wakeful co dition. A sleep stim ulus would now be le effective. With oth stimulus fields, one ca similarly shift fro hunger to thirst o fleeing or brooding a vice versa, or fro courting to fightin mood, etc., but it is unfortunately not possib to arrange the various moods without violen into antagonistic pairs. Like many threa leading from a single knot, they pull in vario directions; a fully neutral basic mood "nil furthermore, apparently does not exist.

With a single mood are associated several be haviour elements, which thus reveal an intern relationship. Thus spontaneous crowing, general expression of masculine self-confidenc very often follows stimulus-induced "win scratching" (Kratzfuss) (Plate III), or calling hen to the nest, or threatening a rival, or peckin The stimulus, so to speak, activates in each ca a specific masculine activity, which ceases wi the termination of the stimulus and leaves be hind only the basic mood "increased manliness which finds expression in spontaneous crowin

When a stimulus-induced mood comes to end, it can also give way temporarily to opposite. All the very varied reactions listed Fig. 19, when they are activated for some lit time and not too intensively, strongly prom crowing as a spontaneous follow-up. Looki through this list, one can designate "moder depression" as common element. This mo then, when set free rebounds into increas "self-esteem"*). After very strong depressio however, crowing does not follow at once, b rather first cackling, as expression of the ov coming of strong tension.

All this gives the phenomenon of mood sh ing a very distinctive character, quite differ from central adaptation, and encourages t suspicion that it might occur at a differe place in the CNS. Here again we have recou

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*According to the motto: "Today I'll give my do treat; first I'll beat him—and then I'll stop !"

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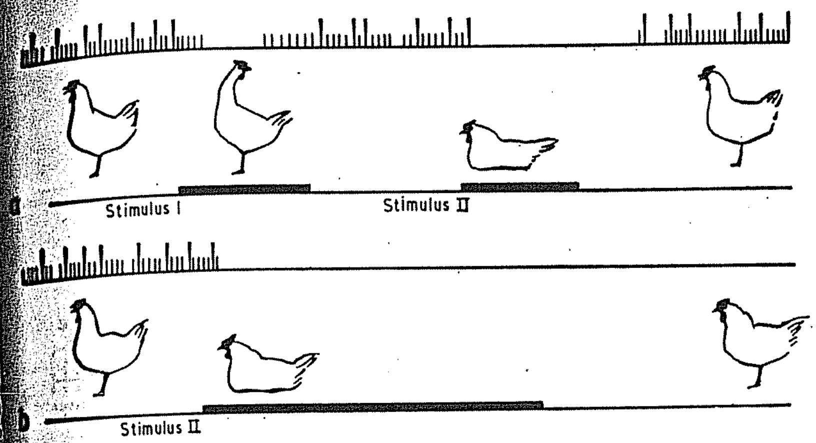

Fig. 18. A fowl, which in consequence of a preceding fleeing stimulus cackles spontaneously and without stopping (kut, kut, kudaw, kut, kut, kut kudaw! . . .' suggested by the upper graph). Stimulus I produces watching out (Sichern), Stimulus II produces sitting down; further explanation in the text.

Watching out
Clucking
Evasion
"Alert call"
Crouching
Jumping
Aiming
Screeching
Cackling

Fig. 19. List of stimulus-released behaviour patterns which are often (in many cases regularly) followed, 5 or 10 seconds later, by crowing. (The "Alert call" is a brief "burst" of cackling and could be roughly translated as "what the devil!" Aiming is a component of fleeing behaviour, cf. Fig. 25 a).

o the experiment with two independent stimulation fields for the same reaction, and ask whether a mood shift produced from one field is also effective for the other or not, and vice versa. In the cases so far examined, as the scheme in Fig. 14a shows, the answer is: yes! This means that the mood shift, unlike the adaptation, takes place *after* the confluence of the two stimulus effects, and thus nearer to the neuromotor apparatus, as Fig. 16c indicates. Thus, since two different processes — mood shifting and adaptation—always affect the behaviour threshold, there at once results the further important conclusion that a given threshold value does *not* always mean the same central situation; for it is clear that much mood shift plus much adaptation can give the same threshold value as a little mood shift plus a little adaptation (see Fig. 11b).

Thus far we have considered adaptation and mood shift isolated from other phenomena. Obviously there are many superpositions. Thus Fig. 20 shows a case of adaptation combined with persistence of the reaction (after-response). We already know that after-response depends on the stimulus duration (see Fig. 10a, b). When, as here with watching out (Sichern), adaptation enters the picture, *no* after-response occurs either with no stimulation or with very long stimulation, that is with complete adaptation. Between these extremes, however, lies a maximum of stimulus effect, so that the values for after-response form a peculiarly bent-back curve.

Fig. 21a shows the effect of a mood shift on a series of experiments with changing latencies. The latency data form a family of curves, which with continued stimulation drift toward smaller and smaller values; here one can, by means of a suitable assumption about the form of the mood shift (Fig. 21c), easily remove this effect, so that the latency data come to lie on a common curve (Fig. 21b).

Closer familiarity with adaptation and mood shifting phenomena greatly eases the interpretation of changing behaviour sequences, which *apparently* have a somewhat arbitrary character. Fig. 22 reproduces such a case, where three identical protracted stimuli bring a cock from drowsiness into a tense-wakeful mood, which expresses itself differently each time. We interpret: the first stimulus (Fig. 22a) produces to begin with a strong fearful tension, which fades

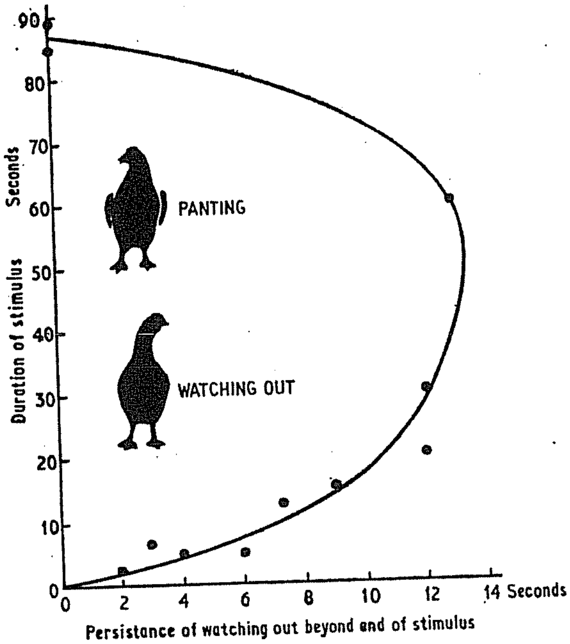

Fig. 20. A fowl which is spontaneously panting (rapid breathing with open beak and wings held away from the body, performed when the body temperature is too high) is caused by stimulation to watch out (Sichern), whereby the panting posture rather suddenly vanishes With a constant voltage (0·5 volt) the stimulus duration was varied; the persistence of watching out after the end of stimulation was measured (after-response). Explanation in text.

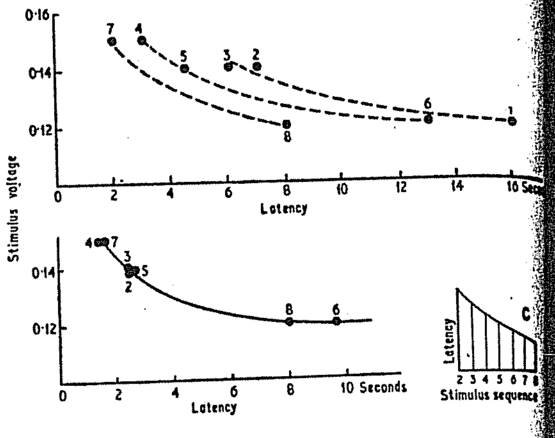

Fig. 21. The way in which the latency of a reactio jumping up and fleeing of a sitting cock—depends on stimulus voltage *and* on the number of previous relea of the reaction. The numbers indicate the sequence of stimulations (Stimulus 1 produced no reaction). In *b* i assumed that the latency becomes shorter by 1/6 in e successive experiment (corresponding to the curve in Explanation in text.

with increasing adaptation, so that the clucking gradually changes over to cackling. The second time, (Fig. 22b) the same stimulus has a lesser depressive effect and therefore rebounds, after its decay with adaptation, to the opposite mood of masculine self-esteem, and then (as we already know) to crowing. Finally, the third time (Fig. 22c), the stimulus effect is so weak that the quickly fading mood hardly rebounds to the other side at all; after a little clucking the cock drops back into his sleepy basic mood, while the stimulation is still going on.

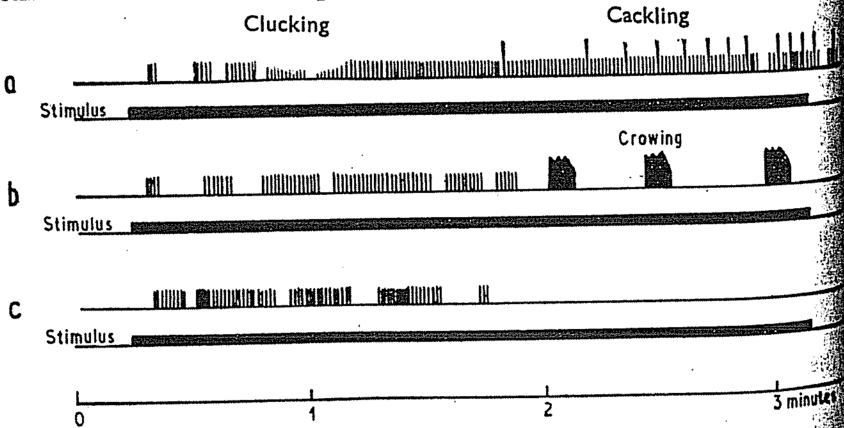

Fig. 22. A cock, in a sleepy basic mood, is provoked to various kinds of activi (clucking, cackling, crowing) by three long, constant stimuli (0, 2 volt) separated brief pauses. Explanation in the text.

Interaction of Different Behaviour Patterns

Against the background of the slowly chan ing moods, the more rapid dynamics of the dri takes place. One can study it experimentally simultaneous activation of two different haviour patterns, either from two stimu fields or from one field combined with an ternal stimulus. The various types of combi tion which can be distinguished are shown schematically in the accompanying table.

Superposition is the simplest and least pr lematic form: both movements remain in pendent. For *averaging* this is no longer tr

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Table I. Types of Interaction of Different Behaviour Patterns.

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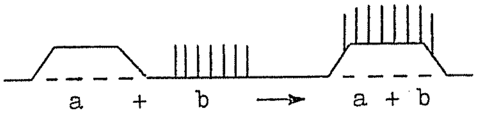
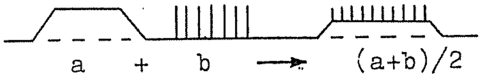
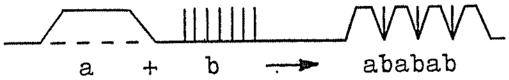
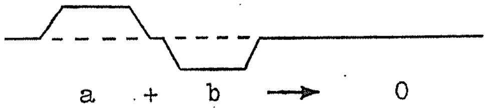
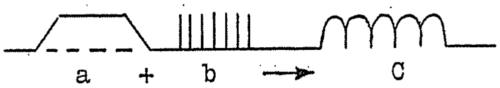
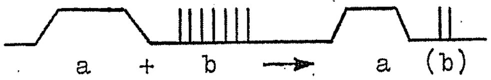
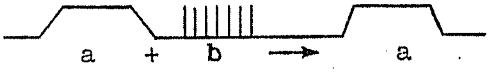
superposition	 a + b → a + b	picking and head turning
averaging	 a + b → (a+b)/2	looking around and watching out
alternation	 a + b → ababab	watching out and eating
cancellation	 a + b → 0	turning to right and to left
transformation	 a + b → c	pecking and fleeing (threat screeching)
masking	 a + b → a (b)	brooding and weak escape
preventing	 a + b → a	immobility and eating, preening, crowing

thus combining rigid watching out (Sichern) with extended neck and attentive looking around (Aufmerken) with large head movements results in looking out with less extended neck and short, sharper head jerks. The more uncommon *alternation* appears when two tendencies are in equilibrium; a good example is eating and watching out, which together can produce an alternation of hasty food-pecking with brief quick raising of the head.

The case of *cancellation* has already been explained with the scheme in Fig. 10 for standing and sitting. This type pertains only to exactly complementary behaviour patterns, such as turning to the left and to the right, which can cancel each other out to zero. For "pure" sitting and "pure" standing this case is actually realized, but for sitting as a part of brooding, standing as a part of food-seeking or of fleeing, the situation is certainly more complicated.

In all of these cases one cannot speak of a "conflict". A clear case of conflict, however, is the "*transformation*" which can appear with simultaneous attack and fleeing tendencies and which shows a new, strongly effective action: tripping about with puffed-out feathers and screeching. The behaviour is very reminiscent of the reaction of a hen on the nest, when something dangerous approaches her. The scheme of transformation, furthermore, well illustrates the drawbacks of forming types: it contains cases of diverse physiological makeup. For example, when one produces a slight fleeing tendency in a hungry animal, so that it ceases to eat, and then gives a sleeping stimulus, which counteracts the fleeing tendency, the animal may then eat for a short time before going to sleep. This would correspond formally to the scheme $a+b = c$ (fleeing + sleeping = eating); but it would be more correct to say: a suppresses c, b suppresses a; $a+b$ liberates c.

This brings us to the next type, *masking*, which is widely distributed. We use this term when one behaviour pattern makes a second one invisible, and it is nevertheless possible to show that the latent drive has not been eliminated. Thus for example sitting down (in broody mood) can completely mask a simultaneous slight clucking excitation. When sitting stimulus and clucking stimulus cease *simultaneously*, however, a few bursts of clucking still follow immediately. Or: fearful "making oneself thin" masks feather-puffing-out; after simultaneous termination of both stimuli the plumage is puffed out for a few seconds. The masked action does, in fact, become visible as an "after-explosion"; its drive must therefore have been present in latent form, but blocked somewhere on its way to the motor apparatus. In most cases, unfortunately, where we suspect masking, such an after-reaction is not visible—which might indicate merely that the visible drive persists longer than the masked one. Here "preventing" is the neutral term. Thus in the case of Fig. 18, where cackling is temporarily interrupted by watching out (Sichern) and sitting down, one can only speak of preventing; it would be clear masking, if the hen cackled more vigorously afterwards. Fig. 13a shows another example of prevention; the defecation provoked by the fleeing stimulus momentarily greatly raises the threshold for clucking, likewise a consequence of the fleeing stimulus.

Which reaction is masked (prevented) by which other ones, usually depends on quantitative factors. We can, however, designate certain behaviour patterns as *dominating*, because they shut off any other activities even when only slightly activated. Such dominating reactions are especially the various forms of fleeing, and still more "freezing"* ("Starre"), against which other behaviour breaks throug only with difficulty.

Measuring the possible *quantitative* effects all behaviour patterns upon each other, throug simultaneous activation in pairs, is an importa step on the way to reconstructing the function organization (Wirkungsgefüge). Fig. 23 giv an example, which shows several things: the o reaction is in this case a posture ("disgu posture"—"Ekelhaltung") which does change with increasing stimulation; pecking a

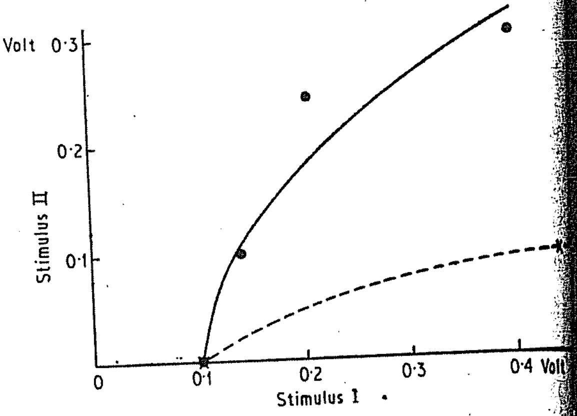


Fig. 23. Dependence of the stimulus threshold for action—picking to the left on the ground and on body (I)—on the stimulus voltage with which a sec action—standing motionless with head stretched ward, saliva flow, and long-persisting unwillingness eat (II), the "disgust posture" (compare Fig. 24, sec sketch)—is simultaneously activated. Stimulus II (gist posture) is first set at a particular value, then st ulus I is added and increased until the correspond actions become visible. X picking movements, ● tur head to the left.

head-turning have thus to contest against *constant* posture of *varying drive streng* One can see that increased "disgust dri raises the threshold moderately for he turning, but steeply for pecking. Thus "disgust drive" seems more strongly con dictory to the pecking drive (which is clos related to the eating drive) than to the neu sideways turning of the head, which can m easily be combined with the disgust posture.

On the whole such experiments indicate among the individual behaviour patterns with the moods—it is generally not possible set up antagonistic pairs; mutual mask (prevention) occurs in very varied gradations

Finally, it may also happen that a stimu does not raise the threshold for another beh iour pattern, but lowers it instead. An examp

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*Freezing, so-called "playing dead", appears in many birds in moments of deadly peril.

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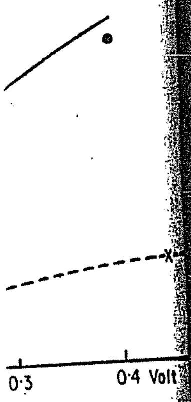

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anxious excited clucking (“kut, kut, kut, kut . . .) of a hen in the farmyard is contagious among the other hens, but does not spread to the cock; he reacts to it with cackling (“kut, kudaw-kut, kut, kudaw”). Likewise, a tape recording of hens clucking produces at most brief cackling in the cock. If one activates in the cock a stimulus field for clucking, it can be seen that his clucking threshold does in fact sink, when he simultaneously hears recorded clucking; in fact, the louder the tape recording, the lower the stimulation threshold. We can therefore designate clucking and cackling as related (allied) reactions; as a matter of fact they do frequently merge into one another, for example in the case of Fig. 22a.

Complex Behaviour Sequences; the Postulate of Level-adequate Terminology

Thus far we have concerned ourselves mostly with simple behaviour patterns, and will now take a closer look at the behaviour sequences into which they enter.

It has already been noted (Fig. 2, bottom) that one can very often obtain different behaviour from a single stimulus field with increasing voltage. From the manifold and varying movement sequences and mixtures of this sort, there clearly appears a type characterized by four features: 1. the sequence of the individual movements is unalterable; 2. one also obtains the sequence (generally) with a constant medium voltage; 3. the sequence is identified as *natural* by the behaviour specialist; 4. the sequence as a whole serves *one* particular function. We conclude from this that we are here stimulating one and the same structure, which activates a drive whose increase excites the individual behaviour components sequentially, corresponding to their individual thresholds.* We shall discuss a few cases.

One particular stimulus field produces in a cock blinking of the left eye at first; if the stimulus is prolonged or increased in intensity, occasional headshaking appears, then wiping the head against the shoulder, and finally scratching the left cheek with the foot. Headshaking and scratching are repeated several times if the stimulation is prolonged enough. It looks as if the cock were being bothered by an invisible fly. Fig. 24 shows another case. The whole sequence here imitates the disgust reaction on mistakenly picking up a (stink-) bug; beak-wiping *after the end* of stimulation is the normal and meaningful conclusion of the cleaning.

In both cases one presumes that a central pathway ascending from the cheek or mouth cavity lies in the stimulation field. Fig. 25a and Fig. 26a give examples of fleeing behaviour from a (non-existent) ground or aerial enemy. Here the stimulus field will lie in the neighbourhood of “higher” pathways, whose activation effects the physiological correlate not of a sensation, but of a form hallucination. Other cases correspond to the activation of specific bodily requirements: Fig. 27 shows the behaviour sequence of falling asleep, or the effect of the “sleep drive”. In the same category belongs the activation of searching for water with subsequent drinking, or search for food with eating, or for instance (in the cock) searching for a spot under cover and creeping in with a long-drawn softly throbbing call: “leading a hen to the nest”.

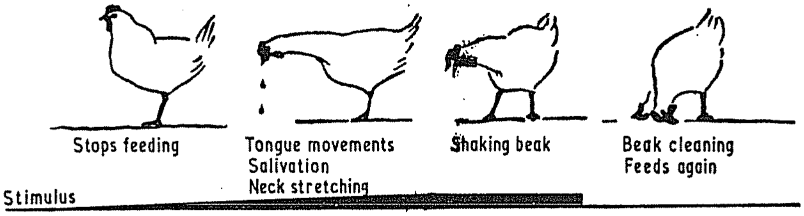

Fig. 24. Activation of a behaviour sequence from one stimulus field. The whole complex serves to remove something unpleasant from the beak. The individual actions except Beak cleaning and Salivation can also be obtained in isolation from other fields of stimulation.

In all such more complex activities, the individual component elements appear in a particular sequence; that does not mean, however, that no element of the sequence can drop out. In fleeing behaviour, all components except the last one can even vanish. This occurs for example when the stimulus is sudden and strong (Fig. 25b), or when another simultaneously strongly activated activity, for example sitting, prevents all but the last element (Fig. 26b). Then the hen behaves like a bird sitting fast on the nest, leaping away only in the last moment of danger.

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*A view long maintained by outstanding students of animal behaviour (Whitman, Heinroth, Lorenz).

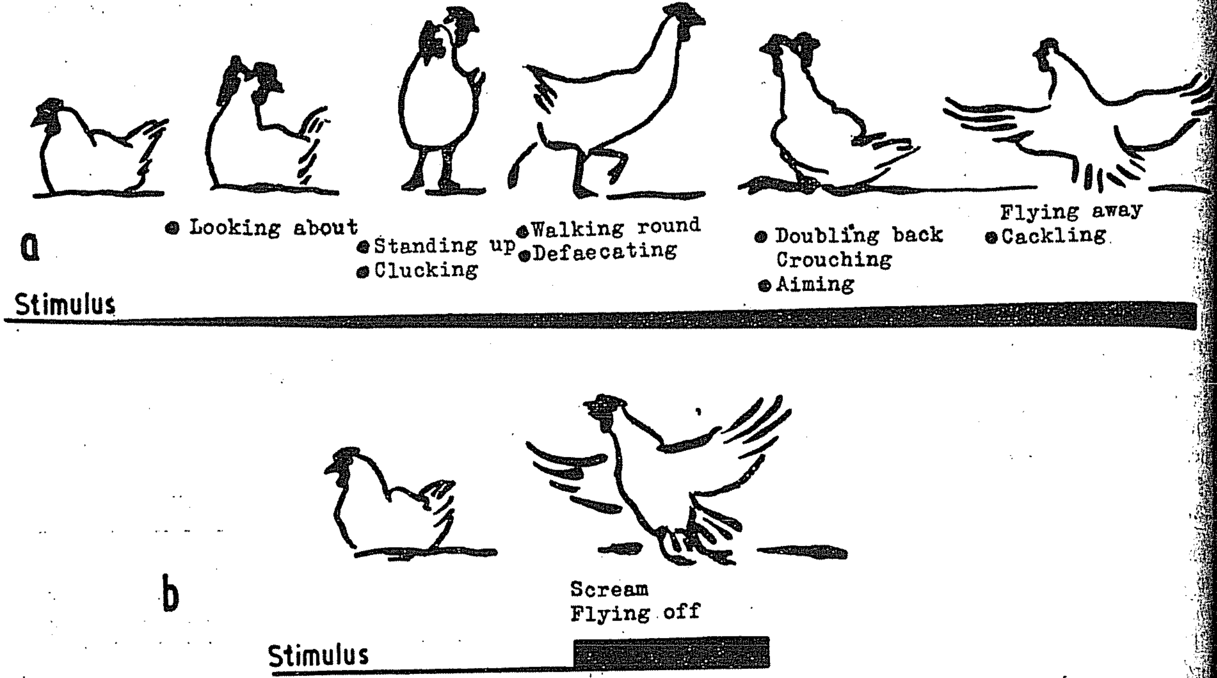

Fig. 25. *a* Behaviour sequence of fleeing from a ground enemy with slowly increasing stimulation of the field (o constant stimulation of moderate intensity); *b* the reaction to a sudden, strong stimulus.

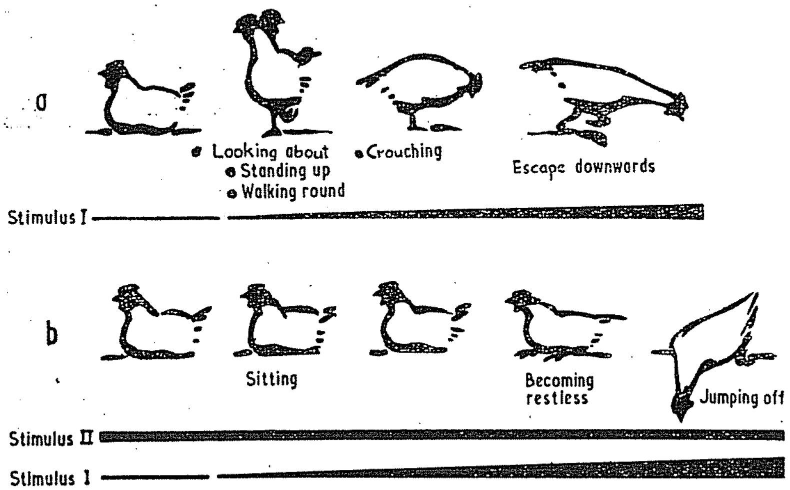

Fig. 26. *a* Behaviour sequence of fleeing from an aerial enemy with slowly increasing stimulation of the field (I); *b* the same with simultaneous stimulation of a second field (II) which produces sitting down.

One can arrange complex behaviour sequences according to various considerations. Whether they are released by the physiological correlate of a sensation, a hallucination, or of a bodily condition (such as hunger or tiredness), is only *one* possible aspe Another consideration is ho far or how completely th are performed without t appropriate external si ation. One easily obtains co plete fleeing behaviour ev in perfectly familiar surroun ings. The behaviour of a co is also complete, when wi increasing stimulus he fi looks tensely into the distanc then fearfully closer and clo by, and finally leaps away the opposite side—exactly if a rat were passing by. a hen one can obtain from stimulation field the true- life behaviour "defendi chicks against a goshaw with wing arching, feath erecting, running around small circles and pierci screeching; living chicks, which the hen question otherwise pecks, are peacefully tol ated with even weak activation of this stimul field.

These are examples of the one extreme;

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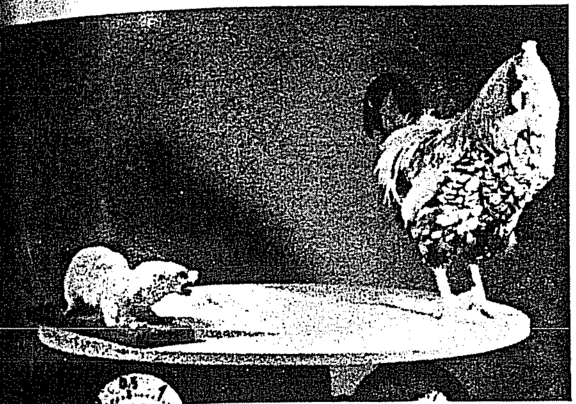
PLATE IV



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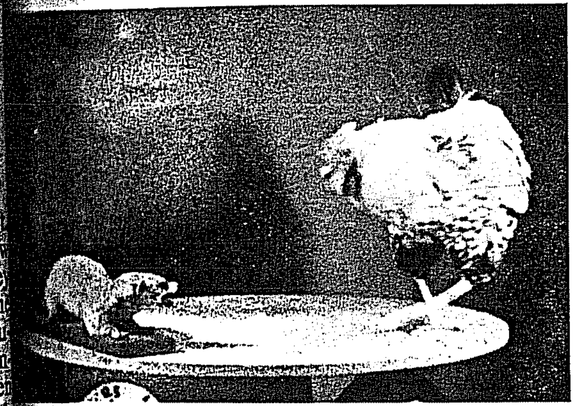

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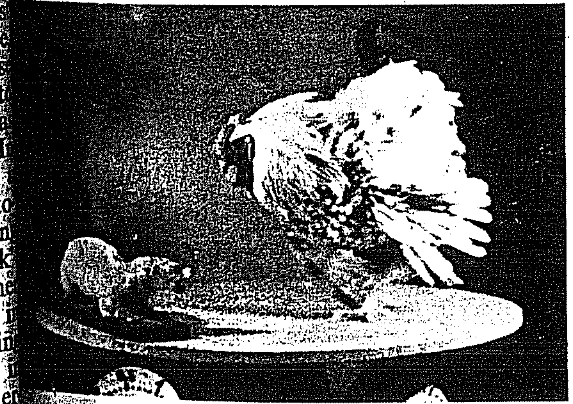

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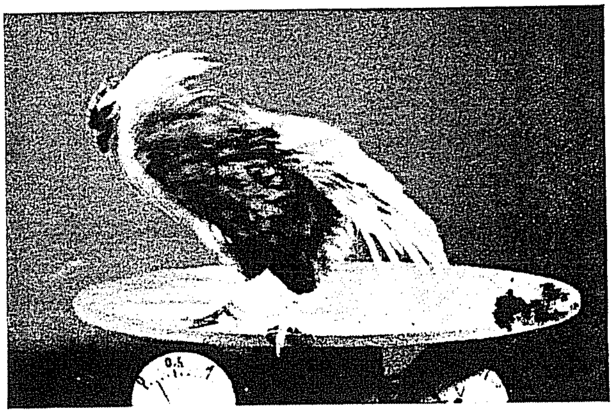
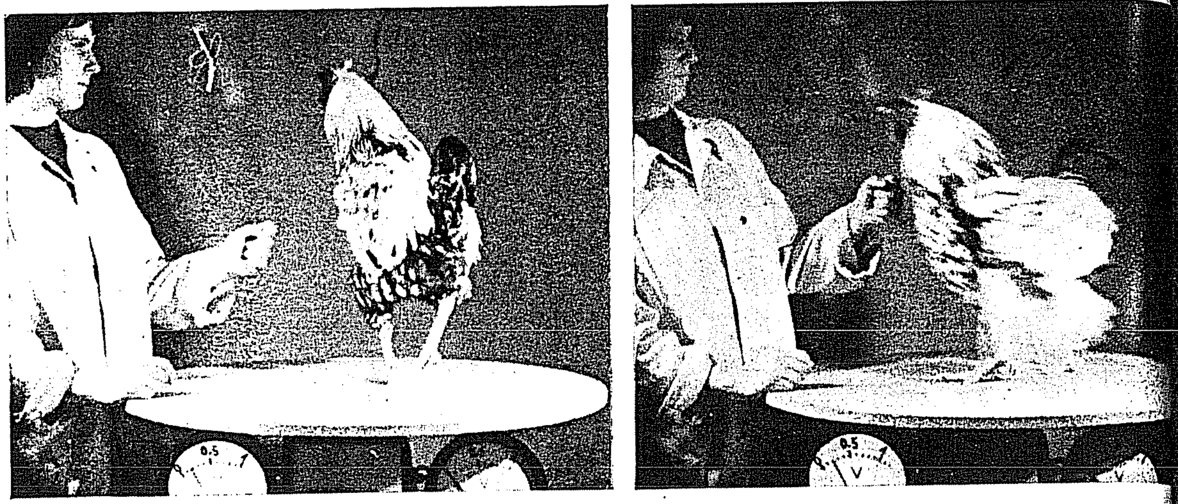


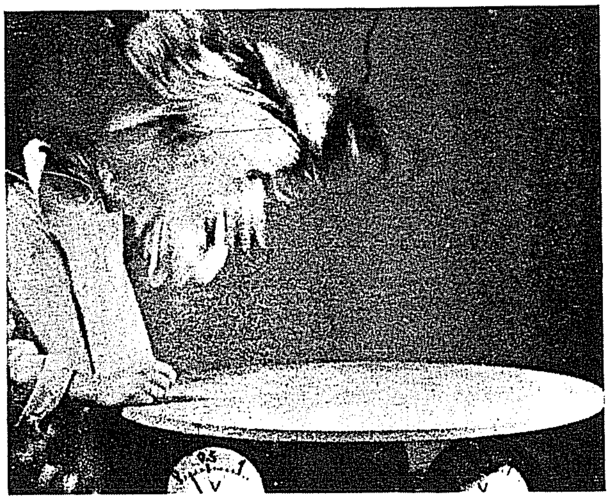
(5)

a. Attack on a stuffed polecat produced by brain stimulation. 1. Before stimulation the cock stands unconcernedly to one side. 2. Stimulation begins, cock advances towards polecat. 3. Full enraged posture. 4. Straight afterwards attack with spurs. 5. The enraged mood continues.

B

PLATE IV (cont.)





b. The same as a; the hesitant attack is made on the face of the normally well-liked handler.

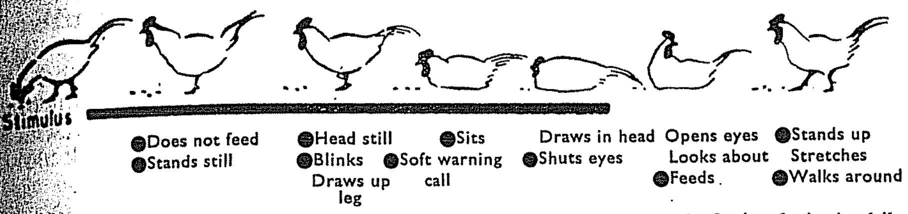


Fig. 27. Behaviour sequence during a sleep stimulus and (after the end of stimulation) while waking up again. The elements designated by ● are obtained in isolation from other stimulation fields.

"vacuum activities", Other behaviour may also take place "in vacuo", but is more intense when the appropriate object is offered; this applies to the "wing-scratching" (Kratzfuss) of a cock (Plate III) in the absence or presence of a hen. Finally, there are behaviour sequences which we have thus far never observed *in vacuo*, such as the attack of a cock upon a rival or an enemy, or in the hen the feather-plucking and pecking of a socially lower-ranking hen. They require at least a suitable dummy as object, and are performed the more expressively, the better the dummy is. Plate IV, a, gives as example the attack of a cock on a stuffed polecat. Lacking a polecat, the next best object is the face of the keeper—not his hand, for that has hen-characteristics (Plate IV, b). Lacking even this object, one sees at most a threat gesture into empty space.

Now it is most noteworthy that all complex behaviour sequences are composed of elements which can also be released in *isolation* from *other* stimulus fields. In Figs. 24-27 those elements which could also be obtained isolated are each designated by a dot. Compared with their appearance in the whole sequence, behaviour elements thus "cut out" often seem automaton-like; a hen which *only* clucks takes on the aspect of a clucking machine; the cock, who shows indefinitely the oscillating aiming movements of the head, as they appear in fleeing only shortly before taking flight, or the cock who from the whole hunger behaviour only shows uninterrupted snapping and swallowing *in vacuo*—and as if the mouthfuls got bigger with increasing stimulus strength—all look as if they had been bewitched into senseless activity! This impression is always strong when the uniformity is great, but adaptation and mood shift are slight.

If one collects the elements which can be isolated from all higher behaviour sequences, it appears that many such elements can occur in quite different sequences. Sitting, for example, can be a part of sleeping or of brooding, or on the other hand be "pure" sitting. Clucking and defecating accompany various behaviour patterns which have the character of anxious tension; cackling is a sign of removal of tension after fleeing as well as after laying an egg; looking around, standing up, and running are common to numerous behaviour sequences; standing ducked and motionless can belong to aerial-enemy behaviour (freezing) or be a gesture of submission to a stronger rival. Even food-pecking on the ground can still be either an element of hunger behaviour or an element of fighting between rivals, where it appears as a threat gesture ("displacement picking"); we have found stimulation fields for both cases, in the second case a rival fight follows at once when one presents another cock (even a stronger one!).

The fact that particular behaviour elements can belong as components to completely different drives (and moods), is theoretically important. It forces us in every case to search for and to *name the highest integrated unit* activated by the stimulus field. For if the terminology does not reflect the synthetizing capacity of the CNS, the reconstruction of the functional organization is made impossible from the beginning. Let us explain this postulate of *level-adequate terminology* more fully with an example. General motor unrest is a common reaction. Only gradually have we noticed that this unrest generally refers to something quite specific. One must vary the surroundings in every possible way to discover the actual goal of the activity. In the experiment in Fig. 28, conspecifics and various other objects were ignored; presenting a fist released slight threatening. A stuffed polecat, fastened to the table, however, *together with* the stimulus, at once produced vigorous threat and attack. Are we then dealing with a tendency to attack an enemy of the species? No, the term is still too specific; for if the stimulus lasts beyond the attack, the hen checks for a moment, turns, and flees screeching. The "resistance" of the (motionless) enemy, but only *together* with the brain stimulation, results in the reversal into flight. The adequate expression for the field, including all

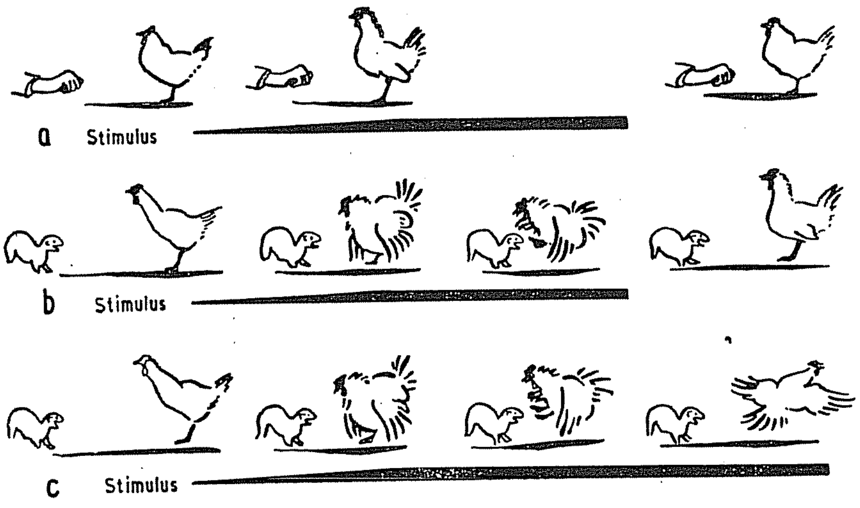


Fig. 28. Releasing ground-enemy behaviour. Without a suitable object the stimulated hen shows only locomotory unrest. Towards a fist she shows only slight threatening (a). A stuffed, motionless polecat is vigorously threatened and attacked; if the stimulus ends at this moment, the hen remains standing and threatening slightly (b); if it does not end, she checks and flees, screeching (c). (After cine film records).

possibilities, must the fore be something lik "ground-enemy beha iour" — in distincti from other fields, whi can produce attack alo or fleeing alone.

The locomotor unre which in the example Fig. 28 is the initial e ment of enemy behavio is in another case in t cock directed only wards the head of a co specific, which is at o pecked (rival fight); a third case towa water, which is dru (thirst), or a hiding pla in which the cock ca (leading to nest), and forth. If one were alwa content with the di nosis "locomotor drive" and then attempted study its relationships to other behaviour, t chances of obtaining comprehensible relati ships would be slight indeed, since we are actuality dealing with the most varied goal appetitive behaviour! The same is true of movements which sometimes appear "pur and at other times as parts of one or anot higher drive.

A Fragment of the Functional Organization

Most of the road to the reconstruction of whole multidimensional functional organiza still lies before us. We will content oursel here with a small segment, in order to sho possible method of proceeding. Our goal only to arrange some behaviour patterns wh contain a common element, clucking. Star point is the experiment already sketched Fig. 14e, with two stimulation fields wh produce "pure" clucking (Fig. 29a, S1, S Next to it is shown the result of a second s experiment, which differs from the first only that here clucking is a part of fleeing behavi so that with increasing drive—we simplify so what—clucking, walking around, and fl away follow one another (Fig. 29b, S1, S We interpret this sequence with different th holds of the individual acts for a common su ordinated fleeing drive, expressed in Fig. 29b crossbars (T) of different length. Finally, take still another experiment, in which,

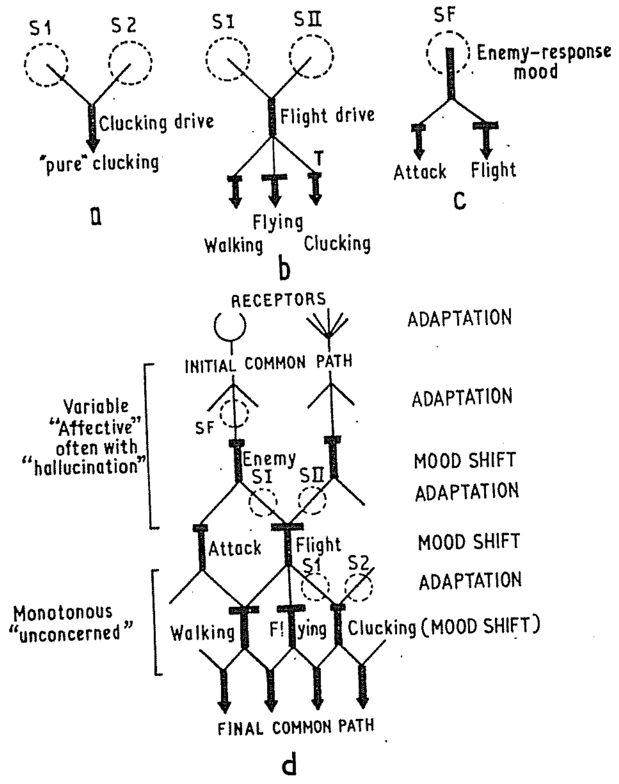


Fig. 29. Sketch of a fragment from the functional organization ("Wirkungsgefüge", control pattern) of some behaviour patterns in the fowl. Explanation in the text.

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time from a single stimulus field (Fig. 29c, SF), threat and attack appear with weaker, fleeing (with all its components) with stronger central stimulation*; which we again explain with different thresholds for the same drive of the behaviour. Thus we have three levels of integration before us, whose arrangement is not open to doubt; Fig. 29d† shows this arrangement. "Pure" clucking lies closest to the motor apparatus, the "final common path" as Sherrington called it. The enemy behaviour lies closest to the sensory apparatus, which we might call the "initial common path". For just as a particular muscle is active in various reactions, a sense organ is involved in releasing various behaviour patterns.

This rough sketch (Fig. 29d) already shows some interesting things. One sees that on the whole a network results, as the doctrine of plasticity demands, but it is a network of *specific* effects. One recognises, furthermore, that to all appearances adaptation and mood shift occur repeatedly in different layers of the CNS. And finally it becomes clear that structures closer to the motor apparatus initiate stereotyped reactions, whereas structures lying closer to the sensory apparatus release behaviour sequences in which the animal "as a whole" appears to be involved.

Another Look at the Localization Problem

At the outset we discovered some facts which made the localization of functions in the CNS problematic: 1. a stimulation field appears "silent" at times, but at other times active; 2. over a period of hours, changing behaviour patterns can be activated from a stimulation field; 3. the same action can often be released from spatially separated fields.

The attentive reader will have remarked that these three phenomena are now physiologically understandable, and in fact necessary.

1. It is to be expected that stimulus fields remain silent when a dominant behaviour such as freezing or fleeing tendency, which suppresses other activity, is spontaneously (and even slightly) present. To say that the stimulus field is "silent" is of course incorrect, since the field is indeed excited, but the resulting activity is blockaded somewhere else. 2. To understand the change of reactions from one and the same field, we refer to two phenomena: the invisible propagation of excitation away from the point of stimulation (cf. Fig. 14d) and the huge variation in the individual thresholds of behaviour through mood shifts and adaptation, with its consequences for the dominance relationships in conflict situations. If one makes the assumption, which is certainly often correct, that the stimulus field includes structures (for example pathways) which belong to different neuromotor systems, and which are all simultaneously —invisibly!—excited, it then necessarily follows that the decision as to which behaviour must become visible is made not in the stimulus field, but *somewhere* else, by the total dynamic situation prevailing at the moment. 3. That identical reactions are to be obtained from different fields follows in part from the circumstance that so many movements are elements of quite different higher behaviour sequences; one thus expects that pathways will lead to such a neuromotor apparatus from various places. On the other hand, this scatter in localization is certainly in part an artifact, resulting from not adhering to a level-adequate terminology. When for example all stimulus areas from which "locomotor drive" can be activated receive this label, no matter whether "pure" motor unrest or thirst-, hunger-, nest-, rivalfighting, or enemy-behaviour—which cannot become visible through lack of the appropriate external object—is involved, then the scattering of localization *must appear* much *larger* than it actually *is*! In concrete terms, we may designate sitting down, standing up, walking, looking around, clucking, defecating, threatening, and so forth as "pure", when neither raising the stimulus to several times the threshold value, nor varying all external factors, succeeds in eliciting anything else. Very often, however, the question remains open, for example because of disturbance from neighbouring structures which are also stimulated; such uncertainly defined stimulus areas are therefore useless for localization.

From the foregoing arise automatically certain precautionary rules for future localization attempts; whoever is interested can easily derive them. It is our conviction that the still puzzling relationship between function and structure must become much clearer if these rules are observed.

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*Anthropomorphically interpreted: the dangerousness of the enemy increases with the strength of stimulation.

†The stimulus field S1, which produces clucking, is only arbitrarily drawn on the pathway leading from the fleeing drive; it might just as well lie in any other afferent path, as long as it is at the same level. The same is true of S1, since fleeing drive is not activated only by enemies.

Conclusion

Perhaps it has become clear to the reader that the construction of a functional scheme of the brain stem activities is indeed a difficult undertaking, but not a hopeless one. Of course monistic doctrines, which try to "explain" "the" function of the CNS according to one formula are useless here. All the more, however, are we moving with our thinking and method of expression into the neighbourhood of differentiated human psychology. It is to be hoped that with closer contact human psychology and the physiology of behaviour will learn from one another; the former, what physiological mechanisms must be taken into account with humans too, and the latter, how one obtains a finer-meshed terminology, better adapted to reality. We do not need to fear that in the process "anthropomorphisms" will sneak into behaviour physiology. It may, however, very well become clear how "theriomorph" man is.

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to the instigation of Prof. W. H. THORPE. The tra
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