THE ANALYSIS OF HABITUATION

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Abstract. Using the “method of continuous data” a detailed, quantitative description of the “action-program” of rats introduced into new environment make it possible to derive indices of the intensity of behavior which correlate closely with hippocampal “theta” activity. Using these indices a mathematical analysis of the course of habituation was attempted. Both uninterrupted and interrupted habituation can be divided into two parts: the activation and disactivation (habituation) curves. The theoretical habituation curve may be represented by a negative (usually) exponential growth function on which intrinsic damped oscillations with exponentially increasing wavelengths and decreasing amplitudes are superimposed (Fig. 11). The activation curve has the inverse characteristics (Fig. 15). The course of positive learning seems to be intimately related to the activation curve. Since the dependence of both the rate of habituation and the rate of discrimination learning on the individual excitability level are of the same nature (inverted U-shaped curves), habituation can hardly be accepted as the simplest kind of learning. For habituation to occur, intervals between stimuli are critical; novelty or absence of reinforcement may be secondary.

INTRODUCTION

For two reasons in the last decade much attention has been paid to the process of habituation: it is a universal phenomenon as well as an experimental model of the simplest kind of learning (26, 29, 31). In this paper the course of habituation will be analysed from point of view of these principles, discussed at the first and especially at the third our meeting (12, 14). Martinek’s paper, this Symposium (22) evaluates the course of habituation in providing typological criteria in dogs.

The ethological or motivational approach puts stress on spontaneous behavior. In contrast to the reflex or S–R approach, which selects short-
term events (reactions) from complex behavior, the ethological approach analyses the nature of long-term behavioral patterns. Therefore the time sequence and duration of all (as far as possible) actions and reactions are registered by means of a method, which I designated in 1963 (13) as the "method of continuous data" (MCD). It facilitates the inductive study of integration of parts into whole. Recently we have introduced a temporo spatial analysis of behavior, which originally was applied for other purposes and in another form by Hediger in 1935 (4). Unlike classical ethology, mathematical description is attempted where possible as proposed by Hull (7). A new approach makes necessary the introduction of new terms, such as: motivational programs or action programs (AP) and motivational potential (E). Both concepts are needed for discussing the problem of measurement of the intensity of behavior. Instead of definitions let me briefly present the methods of assessment for AP and E.

ASSESSMENT OF ACTION-PROGRAMS BY MEANS OF THE MCD

There are three techniques of MCD: (i) time-lapse camera, (ii) tape recording of symbols and (iii) the event-recorder. Figure 1 shows the third most time-saving technique with automatic recording of four reactions, i.e. rearing on hind legs, locomotion in space and the intensity of all

Fig. 1. Diagram of testing box and recording techniques. "Vertical" activity (rising up on hind legs) is registered by means of a Czechoslovak plethysmograph (Prema), the "horizontal" activity by means of "vibration units". All other activities are recorded by two experimenters on an event-recorder RG-300 (Metra).
movements recorded by means of “vibrations-units” (27), which at the same time allows discrimination between scratching and inactivity. All other reactions are recorded by two observers on an event-recorder. At present a system for automatic quantification and mathematical evaluation of more than 50 alternative or parallel reactions has been developed.

Figure 2 shows the AP for two rats placed in a new environment. This representation, which is actually a condensed kymograph record, allows assessment not only of what type of action was performed at any second during 10 min or even hours, but makes it possible to review in a single glance the structure of the whole period of behavior. It is apparent that the four subprograms, i.e. locomotion, rearing, sniffing and manipulation, form a complex — the exploratory program, since they occur together in time and it differs from another complex, the cleaning program where the following subprograms alternate washing, licking, skin-biting, scratching. I would like to stress that it is a question of inductive derivation as to which kinds of action will form a complex. The degree of structuring (2) can be quantified by the statistical method of conditioned probabilities.

The term “program” has several advantages. If scratching is denoted as a reflex, it is automatically considered as an undifferentiated unit, it does not encourage a search for pattern. Scratching as a subprogram implies: (i) that it belongs to a specific, superordinated regulatory structure and (ii) that it is composed of units such as stereotyped scratching, biting at material soiling the fur, and swallowing, all of which draw on the reflex concept.

Within, as well as among, main programs there is an order of events: rats start the cleaning program always with face-washing, the other components follow according to the scheme from above downwards (Fig. 2). Among the main programs there first appears the passive defensive (fear) program, secondly the exploratory, then cleaning, relaxation and finally a sleeping program. Any organism possesses, for any environmental situation an AP; it will always behave in some way. Those environmental stimuli, for which there is no AP, will not be detected. In contrast to computers, the organism has a device which drives it to realize its APs. APs have their own motivational potentials. If the AP cannot be realized, e.g. due to physical confinement or stimulus deprivation, the organism suffers a crisis.

THE PROBLEM OF MEASUREMENT OF THE INTENSITY OF AP (BEHAVIOR)

Within different environments and at different intensities of “tuning” stimuli, or under different motivational potentials, the structure of the AP changes very sensitively. This enables derivation of rational indices
Fig. 2. The structure of the action program for a new environment in a low (rat 77) and highly (rat 42) excitable animals. Duration of various actions expressed on the time axis by length of black rectangles. Interconnecting lines accentuate the sequence of actions. The reliability of observers was checked by simultaneous time-lapse photography (6 sec).
of the intensity of an AP. Inadequate indices of the intensity of reactions may not only markedly distort the process of habituation, but often lead to contradictory conclusions concerning the intensity of drives (5, 23). The lack of knowledge of the structure of AP seems to be the main source of these difficulties.

What does the MCD have to offer? One has at his disposal: (i) the frequency, (ii) the duration of AP and (iii) the physical intensity of movements as reflected by changes in the vertical pressure in “vibration-units”. The exploratory program in rat 42 (Fig. 2) lasts substantially longer, while the duration of single subprograms is shorter than in rat 77. This holds also for the cleaning program. Thus the frequency in a given interval rather than the duration of subprograms is a more sensitive index of speed of movement (energy expenditure). The importance of the maximal frequency values was demonstrated in another way by Martínek (21) in dogs.

Since the intensity of tuning and nonspecific (background) stimuli were the same, the total motivational potential is higher in rat 42. From the physiological point of view the concept of motivational potential is equivalent to the concepts: excitatory potential or excitability (E). It is a functional state which exists before the action of the stimulus. Excitation on the other hand is an on-going process, the intensity of which is modified by the actual intensity of the stimulus. Thus, excitability and excitation differ quantitatively.

Figure 3 shows the physical intensity of AP in rats genetically selected for a high and low nonspecific excitability level (NEL). The exploratory AP is more energy consuming in relation to the cleaning program. Within the cleaning program the most intensive is scratching, second licking and finally washing. Excitable individuals display not only a higher intensity in performing all APs, but they prefer those subprograms which are more energy consuming, i.e. the frequency and duration of scratching is proportionally higher as compared with less excitable individuals. If rats with a low NEL were treated with d-amphetamine (1.5 mg/kg), the frequency and duration of scratching in proportion to washing increased.

Another important correlation came out of studies of the EEG. The more energy consuming an AP, the higher the hippocampal “theta” activity both in duration and frequency (8, 17) (Fig. 3). Since theta activity precedes spontaneous overt behavior by 0.5-1.5 sec (locomotion, rearing, scratching being measured automatically, Fig. 4), it seems probable that synchronized hippocampal activity also reflects the process of “estimation or planning” of the amount of energy which is necessary for performance of a given AP. From the methodological point of view, this enables refina-
Differences in physical intensity of performance of various action-programs as reflected by the vibration units. Rats genetically selected for low (filled circles) and high (open circles) excitability levels have been used. Recording of impulses from vibration units (redirected to several electronic counters by relays) was performed in a standard time interval for all 16 rats. Hippocampal EEG-measurements were performed earlier in another group of rats.

*Hippocampal theta activity*

*Vibration*

**Sniffing**  **Locomotion**

**Time in seconds**

*H*  *V*

**Sniffing**  **Scratching**

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Fig. 4. Hippocampal theta activity (first and third line) precedes spontaneous locomotion (second line) and scratching (fourth line), both measured automatically by means of vibration units.
ment of behavioral indices of the amount of excitement as seem from
the Fig. 5. By giving different weights to the subprograms in the above
mentioned order, one can obtain an index that yields surprisingly close
correlation with hippocampal slow wave activity.

![Graph showing correlations between behavioral indicators of arousal and hippocampal theta activity.](image)

Fig. 5. Correlations between behavioral indicators of arousal and hippocampal theta activity. Arousal in one male rat during first (left part) and fifth (right part) habituation trial. EEG and behavior were continuously recorded during the whole 8-min trial. Duration of specific actions during each successive 20 sec interval depicted on ordinates. Weights for each specific action expressed by size of ordinate scale. Behavioral index of arousal in second line represents weighted sum of all actions. Dotted line represents weighted sum of "vertical" activity and number of squares crossed (scale on right). EEG-frequency analysis performed by means of a Kaiser analyser with six frequency bands. Percentages of the sum of two bands, 3.5-7.5 and 7.5-9.5 cycle/sec during successive 20 sec intervals depicted in first line. Number of impulses from vibration units on last line.

THE INDEX OF RATE OF HABITUATION

If reliable indicators of the intensity of behavior have been obtained, incorrect conclusions may come from inadequate indices of rate of habituation as stressed also by Hinde (6). There are at least seven parameters in the habituation curve (small latters in Fig. 6A) which may vary under different experimental conditions. The commonly used index d (absolute decrease in response strength) does not discriminate among habituation curves 1-5 (Fig. 6BC). These curves discriminate another commonly
applied index $t$ (time or number of presentations necessary to reach a selected criterion), which on the other hand does not discriminate among curves 6–8 (Fig. 6D). The index $d'$ (relative decrement) is the more unreliable, the more it approximates to the limit of 100%. The index $f$ (size of the area) does not discriminate between curves 9, 10 (Fig. 6E). What does the mathematical description offer? First it is necessary to take into account that habituation curves are nonlinear functions. In most cases the course of habituation can be expressed by an exponential function, exceptionally by a hyperbolic function (Fig. 6F). Thus the semi-logarithmic, or log-log transformation (rectification) enables one to obtain, instead of six less reliable indices, two constants $a$ and $b$ which fully describe the curves. The constant $b$ expresses the true, relative rate with which the empirical data approximate zero independently of the $a$-value. Thus the basic presumption of comparability is fulfilled. The next section will deal with the physiological meaning of the constants $b$ and $a$ and of the parameter $o$.

**STRENGTH OF STIMULUS OR INITIAL EXCITEMENT AND THE RATE OF HABITUATION**

Relations among the three parameters will be analysed in two kinds of habituation: “uninterrupted” and “interrupted”, i.e. during continuous and repeated stimulation. In the first case, the waning of exploratory
activity is studied in equidistant time intervals during one session, in the second case changes in the weighted sum of exploratory activity per 10 min test is followed by repeated exposure of rats to the same environment.

Of the nine characteristics of habituation listed by Thompson and Spencer (30) attention will be directed to the relationship between intensity of stimulus (or excitatory potential) and rate of habituation. It has been shown that the higher the stimulus strength, the lower the rate of habituation (3, 5, 6, 10). Taking into consideration that this relationship is not a linear one (a fact often ignored), a theoretically important question emerges of whether a further decrease in the intensity of stimulation would cause the regression curve to continue either according to an inverted U-shaped curve, or would asymptotically approximate the highest rate of habituation. Two approaches are open. Since the intensity of a reaction is a function of both the stimulus intensity and the level of excitability, i.e. \( iR = f \left( \frac{iS}{iE} \right) \), it follows that the same relationship should be expected if \( iE \) will be varied and \( iS \) held constant. Both, the natural (constitutional) and the experimental variations in \( iE \) yielded similar results. As seen from the Fig. 7, the higher the individual excitability level (NEL), the higher the rate of habituation up to a certain level and than it decreases with increase in the NEL. The right-hand part of this inverted U-relationship is in agreement with the results obtained by variations in the \( iS \). Further experiments are necessary to prove whether variations of the \( iS \) (first of all low \( iS \)) will also give the

![Fig. 7. Dependence of individual differences in rate of uninterrupted habituation (ordinate) upon excitability level (abscissa). Rats were stimulated by switching off illumination for 1 min (six times in all) with 3 min intertrial intervals. Maximum frequency of exploratory activities per trial served as the index of the excitability level. Filled circles represent data for individual rats.](image-url)
same picture. This type of relationship has been observed repeatedly under very different conditions of interrupted and uninterrupted habituation. However, this broad zone of variability was always apparent. Some suggestions concerning the reasons for this broad variability will be mentioned later.

Figure 8 shows the results of pharmacological changes in excitability (20). Under the influence of d-amphetamine (1.5 mg/kg), rats are aroused faster, the level of maximal excitement is higher and the rate of uninterrupted habituation is slower in comparison with controls, whereas under chlorpromazine (3 mg/kg), the time to reach maximum arousal is greater, the absolute level is lower, but the rate of habituation is also slower than controls. Again, there is an inverted U-relationship. The same picture appeared if excitability levels had been changed by means of combined nutritional and endocrinological treatment (16). However, there are hormones and drugs that induce dissociation (Fig. 9). Chronic application of hydrocortisone (80 mg/kg) even facilitates to some extent the initial excitatory phase and at the same time accelerates uninterrupted habituation especially in highly excitable individuals (19). Anticholinergic drugs such as scopolamine or 3-quinuclidyl benzilate seem to produce similar effects (9, and N. Rosić, personal communication).
The following conclusions can be drawn from the above mentioned results: (i) The constant $a$ seems to reflect, under certain conditions $^1$, the E-value and the efficiency of the excitatory (activating) system, while the constant $b$ is closely related to the inhibitory (disactivating) process. (ii) If a linear relationship should exist between the intensity of activation and the rate of its waning, a unifactorial explanation would be possible. The inverted U-relationship, and dissociations suggests a bifactorial explanation (3, 15). (iii) The existence of dissociation, i.e. simultaneous enhancement of both processes, may help to explain one source of the broad variability in Fig. 7; on the other hand, it is important for regulation of the learning process by means of drugs. The inverted U-shaped relation between excitability levels and rate of discrimination learning was observed many times (13, 16). This is actually another expression of the more than 60 year old Yerkes-Dodson law (32). A number of drugs and other treatments, which have been shown to improve learning, could exert their effect in a nonspecific, or pseudospecific way by changing primarily the excitability level. A drug “for learning” should alter the relationship in Fig. 10 as indicated by the hatched areas. (iv) Similarity in the shape of the dependence of both the rate of habituation and the rate of discrimination learning upon the iE suggests that habituation can be hardly accepted as the simplest kind of learning. It appears simple only from the point of view of sensory input. There exists an one-trial learning, but an one-trial habituation never has been observed.

$^1$ The computed constant $a$ at point 1 of the abscissa rather than at 0 level reflects the individual E-value, provided that normal (well rectifiable) habituation curves have been obtained.
DAMPED OSCILLATIONS IN THE HABITUATION CURVES

The last part of this paper will deal with a new (tenth) characteristic not included in Thompson and Spencer's list. As mentioned above (see Fig. 6) besides the constant a, b, the parameter o, may vary. These oscillations around the smooth regression curve have been considered as being caused by irrelevant factors (7, p. 261) and therefore uninteresting. However, Oswald (25) and Morell and Morell (24) noticed that the "fluctuations" seem to be intrinsic closely associated with decrease in vigilance. A description of the quantitative characteristics of these "fluctuations" remains.

As seen from Fig. 11 the mathematical analysis of the average course of uninterrupted habituation led to the conclusion that the theoretical curve of habituation seems to be represented by an exponential function with superimposed damped oscillations having the following characteristics: a (presumably) linear decrease in amplitude and an exponential increase in wavelength.

In some individuals the exponential occurrence of "excitatory-waves" could be observed even in exploratory subprograms during the temporo spatial analysis of locomotion (Fig. 12). One "round up" in the box appears on the kymograph in the form of a trapezoid. As can be seen, the intervals between rounds increase exponentially. Thus, it is possible to predict the time at which the rat will decide to make a "round" (arrows indicate the computed value). No less important is the opposite case (last line) where usually at the beginning of the experiment, the intervals between rounds decrease exponentially and thereafter increase. Transient states make the impression of irregularity.

The theoretical curve described for uninterrupted habituation holds also for interrupted habituation. However, the quantitative characteristics...
The analysis of habituation

Time in 4 min blocks

Fig. 11. Derivation of the theoretical habituation curve. Thin and dotted lines in upper graph demonstrate average uninterrupted habituation of exploratory activities in two groups of rats (n = 12 + 12) of the same age (2 months), treated in the same way, but tested at different times (6 months later). Both groups selected from a large sample of rats in the same way, i.e. to ensure in each group four individuals with a low, four rats with a medium and four with a high NEL-values. Since the average course of habituation is much the same in both groups, all 24 rats were averaged (heavy line). Middle graph: semi-logarithmic transformation of average curve with regression curves and with interpolated oscillations. Lower graph: damped oscillations in antilogarithmic form.

of oscillations are less pronounced probably due to the momentary functional state at the time of stimulus presentation. Further investigation is needed for clarifying why some individuals display all described characteristics while others do not.

Some other data facilitate the physiological interpretation of damped oscillations. Figure 13 demonstrates that the higher the initial rate of interrupted habituation, the higher the subsequent excitatory wave. It appears as if the system first exaggerates the inhibitory phase thus provoking the opposite process — the exaggeration of the excitatory phase, until by means of damped oscillations the appropriate slope is found. This holds also for uninterrupted habituation (Fig. 14). Here it can be seen that the rat runs with high oscillations which appeared clearly in the vibration-scores. In individual subprograms they are not necessarily apparent.
Fig. 12. Time-space analysis of locomotion in the experimental box (75 × 55 cm) with transparent fence to prevent crossing of middle squares. One “round up” in the box appears on the kymograph record in the form of a trapezoid (scheme in right upper part). Occurrence of rounds in time during 2.5 hr is presented for four males. Rounds may appear single or in bouts of 2, 3, 4, rounds which form a system with characteristic time relations (see male rat 45). Arrows indicate time at which a round or a bout of rounds should occur provided that intervals between them increase exponentially.

It is known that over-driving of the inhibitory process leads to disinhibition (26). During acceleration of habituation by shortening the intervals between stimuli, or during “over-extinction” or “over-habituation”, an “explosion” of the excitatory potential was often observed in our Laboratory. The phenomenon of damped oscillation and “over-habituation” suggests again that habituation cannot be explained by unifactorial theories of Lorenz and Hull who both assume for contrary reasons, a continuously smooth decaying curve (15). Neither the exhaustion of the excitatory potential or substances (Lorenz), nor the accumulation of the inhibitory potential of substances (Hull) may explain the quantitative characteristics of the course of habituation.

Pharmacological alterations in the size of oscillations offer additional support for bifactorial explanation (20). An increase in the size of oscillations occurred in both cases, if genetically excitable rats were treated with chlorpromazine (3 mg/kg) and low excitable rats, on the contrary were treated with d-amphetamine (1.5 mg/kg). The combination: excitable
Fig. 13. Relationship between initial rate of interrupted habituation and amplitude of first recovery wave. Intermittent photic stimulation as described in Fig. 7 was used. Correlation coefficient between the two variables yielded $r = 0.785$, $n = 75$.

Fig. 14. Individual differences in size of oscillations during uninterrupted habituation to continuous photic stimulation.
rat + excitatory drug, or low excitable rat + depressive drug led in both cases to a decrease in the size of oscillations. If the excitatory and inhibitory potentials are equally strong, the system produces oscillations which are the greater, the higher both potentials. If one of them dominates, oscillations decrease.

The EEG-analysis revealed that the neocortex seems to play an important role in the occurrence of oscillations (17). A positive correlation ($r = 0.767$, $p<0.02$) has been found between interindividual differences in the size of oscillations and the amount of rhythmic spontaneous spindle (or spike-wave) discharges in ECoG. Individuals with high oscillations also seem to display an unstable and in general a lower level of performance during learning (16). They are, therefore termed "labile".

**DYNAMICS OF ACTIVATION**

Finally some remarks need be made concerning the dynamics of the activation (excitatory) process by means of which habituation is initiated. Usually this process is so quick that there is little opportunity for a detailed analysis of the activation curve. In those individuals which reach the maximum of excitement later, oscillations can be observed with exponentially decreasing intervals (Fig. 12, last line). This is sometimes also apparent in the cumulative record of the exploratory reactions during the first minute of exposure of rats to a new environment. The theoretical curve of habituation could therefore be completed by the activation curve with the following characteristics: oscillations with exponentially decreasing wavelength and increasing amplitude are superimposed upon a positive exponential function (Fig. 15). Fourteen years ago (11) intrinsic

![Figure 15. Schematic representation of a theoretical activation and disactivation (habituation) curve. For explanation see text.](image-url)
oscillations were described in the elaboration of classical conditioned reflex. Thus there is a correspondence between the course of habituation and extinction (disactivation) on the one hand and activation and positive learning on the other hand.

The universality of the above mentioned quantitative characteristics of habituation is very impressive. These characteristics can be observed at the neuronal level, in the autonomic nervous system, or at the complex motivational level (see empirical, not interpolated data of Adrian’s and Rosenbluth’s curves (1, 7, 28)). The similarity in quantitative characteristics, of course, does not mean identity of underlying mechanisms. It reflects rather the similarity of basic regulatory principles and as such it is of great heuristic value.

The same relationships found in interrupted and uninterrupted habituation suggests that interrupted habituation might be considerer as a special case of uninterrupted habituation.

The above mentioned results throw some doubt on the adequacy of current definitions for habituation. For the process of habituation to occur the presumption of the novelty of the stimulus (orienting reflex) does not seem to be essential. Unconditioned stimuli and reactions do habituate (14). Habituation will appear if known stimuli are applied (15). What is critical is only the interval between stimuli. For the process of habituation to occur, the presumption of the absence of reinforcement also seems not to be essential — apart from the fact that proof of the absence of reinforcement is extremely difficult. Habituation and spontaneous recovery will appear in continuously reinforced reactions. Pavlov (26) already recognized this fact and called it: the inhibition from reinforcement.

REFERENCES


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