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FURTHER PROPERTIES OF THE ALTERNATION CONDITIONED REFLEXES IN DOGS

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In the previous paper of this series (Szwejkowska et al. 1964) the analysis of the instrumental conditioned reflex (CR) alternately reinforced and not reinforced by food was carried out under conditions of constant intertrial intervals. It has been shown that, in this condition, no true alternation can be established since the animal's responses to the conditioned stimuli (CSi) are determined by the time which elapses after the preceding positive trial, or, more generally, after the last presentation of food. Thus, when the CS is presented after the double interval from the preceding positive trial, it produces the positive response. On the contrary, if within a short interval after the positive trial the CS is presented several times, all the responses to it are negative. The conclusion has been drawn that the termination of the act of eating produces an inhibitory after-effect whose duration is determined by the intertrial intervals and which gradually subsides when the moment of the next positive trial approaches.

The question arose as to whether the dogs are able to solve a true alternation problem in that case when by introducing the variable intertrial intervals the time factor would not provide any cue for its solution. This is the subject of the present paper.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were performed on 5 dogs in the sound-proof CR chamber. Since dog No. 5 could not master the task required and developed experimental neurosis he was not included in this report.

First, the animals were taught to lift the right foreleg and place it on the food-tray in response to the presentation of a buzzer under food reinforcement. When this task was solved the buzzer was no more presented, and a new stimulus, a metronome, was introduced instead. From then onward the metronome was reinforced by food only on every second presentation.

In consonance with the Wyrwicka's finding (1952), the instrumental response to the metronome was nearly immediately transferred and was then performed on its every presentation. In positive trials, the food was presented after the performance of the trained movement. In negative trials, the CS lasted 5 sec. irrespective of the animal's response. Eight positive and 8 negative trials were given in each session. The act of eating in positive trials lasted about 10 to 20 sec.

When the animal did not perform the trained movement in the positive trial, the food was presented "gratis" after 5 sec. of the operation of the CS. This was scored as a positive-trial error. On the other hand, if the animal performed the trained movement in the negative trial this was referred to as a negative-trial error.

Further details of the procedure are presented below.

RESULTS

Part I

Preliminary alternation training. During this training the intertrial intervals were constant and their duration was 1 min. Twenty five sessions, consisting, in total, of 200 positive and 200 negative trials, were given.

Table I, row „a", represents the number of positive-trial errors in each dog in blocks of five sessions, row „d" represents the same for negative-trial errors. The average of errors for all the dogs is represented in Fig. 1 „a" and „d" respectively.

It may be seen that the number of errors in positive trials is very low and drops practically to zero in the fifth five trial block. On the contrary, the number of negative-trial errors is conspicuous in the first and the second blocks and only then begins it to fall reaching, in average, less than 15 per cent in the fifth block.

First alternation test. From the 26th experimental session on the intertrial intervals, instead of being stable, became variable, changing from 0.5 to 2.0 min. according to the fixed schedule presented in Table II. Since it was not proper to present the successive negative CS too soon after the act of eating, the intervals after positive trials lasted from 1 min. to 2 min., while intervals after the negative trials lasted from 0.5 min. to 1.5 min. Twenty five sessions were given in this series of experiments.

Table I

Number of errors in successive 5 session blocks in individual dogs to positive and negative stimuli

Dogs	Successive blocks	Positive trials			Negative trials		
		Preliminary test	Test I	Test II	Preliminary test	Test I	Test II
		a	b	c	d	e	f
1	1— 5	0	3	0	40	21	9
	6—10	2	1	1	26	12	10
	11—15	1	3	3	13	5	9
	16—20	1	1	2	9	2	6
	21—25	0	1	0	9	5	6
2	1— 5	5	3	1	30	23	6
	6—10	3	1	0	32	23	6
	11—15	1	3	2	12	9	6
	16—20	0	0	1	8	7	3
	21—25	0	0	0	5	7	5
3	1— 5	0	5	2	40	27	8
	6—10	0	3	1	40	18	8
	11—15	2	1	1	30	13	4
	16—20	1	2	9	13	10	2
	21—25	2	2	5	4	5	2
4	1— 5	17	0	2	13	25	5
	6—10	4	1	1	12	21	4
	11—15	0	1	0	6	12	7
	16—20	1	2	1	4	6	6
	21—25	0	2	0	2	5	4

Table II

Kinds of tests

Tests	Trials															
	1 +	2 −	3 +	4 −	5 +	6 −	7 +	8 −	9 +	10 −	11 +	12 −	13 +	14 −	15 +	16 −
	Interwals in min.															
Prelimin. test	—	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Test I	—	1.5	1.0	1.5	1.0	2.0	1.0	1.5	0.5	2.0	1.0	1.0	1.0	1.5	1.5	2.0
Test II	—	2.0	1.5	1.5	1.0	1.0	1.0	0.5	2.0	1.5	1.0	2.0	1.0	1.5	1.0	1.5

+ positive trials; − negative trials

The results of this test are presented in Fig. 1 „b" and „e" and in Table I, rows „b" and „e". It may be seen that there is a small but quite distinct rise in the number of positive-trial errors, and much larger increase in the number of negative-trial errors. While the number of posi-

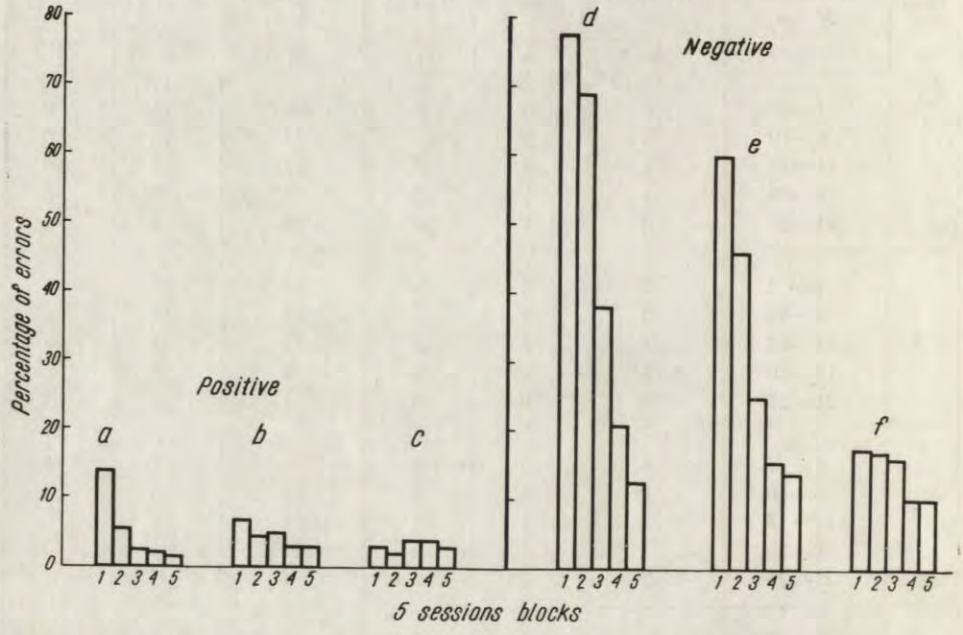

Fig. 1. Percentage of errors in successive blocks in individual dogs to positive and negative CSi. Abscissae, 5 session blocks. Ordinate, percentage of errors; a, b, c, positive trials; d, e, f, negative trials; a and d, preliminary training; b and e, first test training; c and f, second test training.

tive-trial errors remained at the same level throughout the entire series, the number of negative-trial errors dropped significantly reaching nearly the same level as that obtained at the end of the preliminary alternation training.

Second alternation test. In the successive 25 sessions, the intertrial intervals were again variable but according to a different schedule than that applied in the first test (Table II). The results of this test are presented in Fig. 1 „c" and „f", and in Table I, rows „c" and „f".

We see that the errors in the positive trials remain at the very low level except for one dog in which they increased at the end of the series. The number of negative-trial errors after the change of schedule remained practically at the same level as that in the last block of the pre-

ceding series. In the following blocks it slightly decreased reaching about 10 per cent of all trials.

Comment. The results of these experiments show that the change of the experimental schedule, consisting of replacing the variable intervals for the stable ones, causes a strong deterioration of the animal's performance. In agreement with our previous data (Szwejkowska et al. 1964), this indicates that in the preliminary training the animal learnt to react to the time factor rather than to the alternate sequence of the CS. However, the animals gradually improved their performance showing that they were quite able to master a true alternation task. The fact that the change of the interval's schedule from test I to test II did not affect the animal's responses suggests that the solution of the problem was not based on acquiring the stereotype of behaviour adjusted to the first schedule.

Part II

Distribution of errors in the first and second alternation test. Both tests consisted of 50 sessions in which the number of positive-trial errors did not undergo major changes, although it was higher than that at the

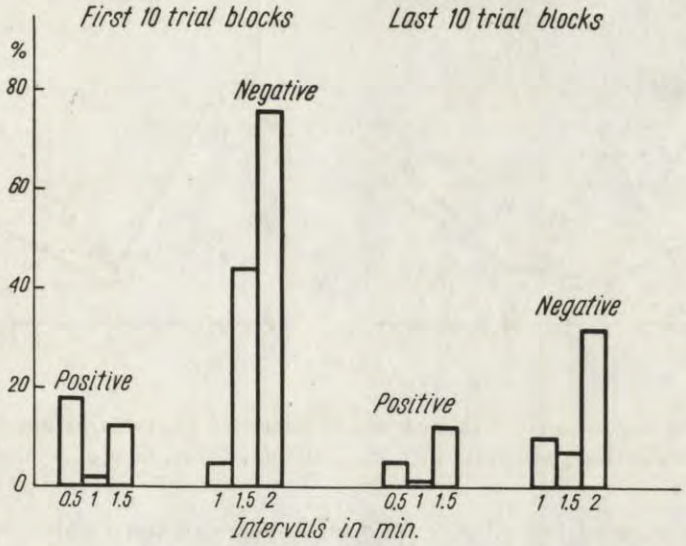

Fig. 2. Distribution of errors in positive and negative trials at particular intervals for the first and last 10 trials of the series. Abscissae, intervals in min. Ordinate, percentage of errors.

end of the preliminary alternation training the number of negative-trial errors increased significantly at the beginning of the tests and then fell to about 15 per cent of all negative trials. In order to find out what is the relation between the number of errors and the intertrial intervals, in Fig. 2 the distribution of errors in positive and negative trials at particular intervals is represented for the first and last ten trial blocks.

It may be seen that at the beginning of the application of the variable intervals schedule the majority of positive-trial errors occurred at the minimal (0.5 min.) interval between the negative and positive trials. On the contrary, the majority of negative-trial errors increased with the length of interval separating the negative trial from the preceding positive trial. This increase, although much less accentuated remained up to the end of both series.

Third alternation test. After terminating all the previous series of experiments the equal intertrial intervals were again introduced in each session, but those intervals were different in different sessions. Altogether 3 to 7 sessions were given with intervals of 0.5, 1.0, 1.5 and 2.0 min.

The results of these experiments for each dog separately are presented in Fig. 3. It appears that the numbers of positive-trial errors are

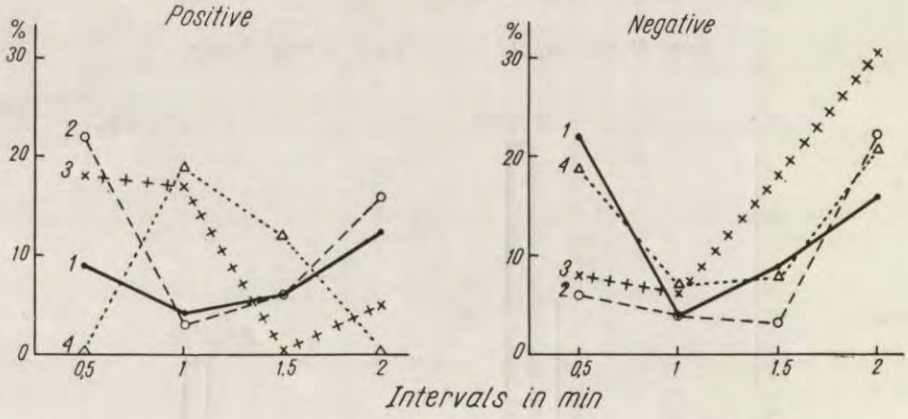

Fig. 3. Third alternation test with equal intertrial intervals in individual dogs. Abscissae, intervals in min. Ordinate, percentage of errors.

evenly distributed for all intervals, although different animals have preference to errors after particular intervals. Thus dogs Nos. 1 and 2 committed most errors after 0.5 min. and 2 min. intervals, while dog No. 4, on the contrary, commited least errors after these intervals; in dog No. 3 the maximal number of errors was after 0.5 min. and 1 min. intervals.

Much more regular was the distribution of negative-trial errors. The curves in all the dogs have two peaks, one at the 0.5 min. interval, the other one at 2 min. interval.

Comment. From the data concerning the distribution of errors in relation to the intertrial intervals the following conclusions may be drawn. In the positive trials, the most difficult interval separating them from the negative trials was the interval of 0.5 min., while, in the negative trials, the most "dangerous" for the correct response was the interval of 2 min. However, when in the third test the 0.5 min. intervals were introduced, the number of errors in negative trials was larger than that at 1 min. and 1.5 min. intervals.

DISCUSSION

The problem raised in this paper was whether the dogs are able to establish a true go-no go alternation, in which a positive trial would be the cue signalling that the next trial will be negative, and, *vice versa*, a negative trial will be the cue signalling that the next trial will be positive. The answer to this question was in affirmative. Although no dog of our group was able to solve the problem without errors, their performance at the end of the test was well above the chance level reaching in average 90 per cent of correct responses. Moreover, even the most drastic changes of the intertrial intervals schedule from day to day, occurring in the third test, did not affect the animal's performance.

Let us analyse which mechanisms are necessary for the solution of this problem, as compared with those mechanisms which were in operation with fixed intertrial intervals.

After the positive trial, or after the act of consuming food, the inhibitory after-effect develops which determines the negative character of the next trial. Therefore, the shorter, to some extent, the interval between the positive and negative trial, the easier is the inhibitory response in the next negative trial and the "disinhibitory errors" are less numerous. The longer such interval, the weaker the inhibition, and the more difficult is the task to inhibit the response in the succeeding trial. The only exception in this rule is provided by the case when the negative trial follows nearly immediately the act of eating. This happened when in the third test the intertrial intervals were reduced to 0.5 min. The disinhibition of the response occurring in this condition is undoubtedly due to the increase of alimentary excitability which, as it is well known, is manifest in a hungry animal just after the act of eating. Thus the un-

conditioned facilitatory effect of the termination of the act of eating overshadows the inhibitory after-effect developed by the conditioning procedure.

Quite different is the situation in respect to the cues determining the positive trials. When the intervals between trials were constant, as was the case in our previous study, the cue for the positive trial was simply provided by the lapse of time. In consequence, even several inhibitory responses were elicited by the CSi crowded within a short time after the act of eating. However, when the intertrial intervals are variable, such solution of the problem is not possible, and the animal has to develop another tactics, namely that of canceling the inhibitory after-effect when the negative trial is over, quite independent of the time elapsed from the last reinforcement.

It is clear from our experiments that the dogs are quite able to do so, the condition which is indispensable for the solution of a true alternation problem. This task is not an easy one, as judged from the increase of the number of errors in positive trials following, at short interval, the negative trials. However, this difficulty may be partially overcome by the appropriate training, as may be judged from the improvement of the animal's performance in this respect at the end of the second test series. Nonetheless, the difficulty seems to be permanent, since the number of errors in positive trials rises again in the third test in those sessions in which the intertrial interval is 0.5 min.

On the basis of these considerations, it becomes clear why the true alternation, as required in the present experiments, is more difficult than the fixed interval pseudoalteration, required in the previous study. It was noteworthy that while in the previous study the eventual number of errors in positive trials was zero and in negative trials not more than 6 per cent, in the present study the number of positive trial errors was about 3 per cent, and that of the negative-trial errors 10 per cent. The only problem to be solved by the animal in experiments with the constant intervals schedule was to develop the inhibitory effect covering the next trial after each positive trial. On the contrary, the task to be mastered in experiments with variable schedule is for one thing to prolong this inhibitory effect when the intertrial interval after the positive trial is protracted, and for another, to cancel this effect immediately when the inhibitory trial is over. The difficulty of the second task may be manifested by the results obtained in our previous study showing that the CS given in the negative trial not only does not cancel the inhibitory phase but on the contrary tends to increase this phase (cf. Szwejkowska et al. 1964).

SUMMARY

1. The problem of go-no go alternation in alimentary CRs under the condition of variable intertrial intervals can be solved by dogs, although it presents some difficulty for the animals, and never the 100 per cent, performance is reached.

2. The most frequent errors in the positive trials occur when the intertrial interval is very short, i.e., when the positive trial is separated from the negative trial by 0.5 min. The most frequent errors in the negative trials occur when the interval separating them from the positive trials is long, amounting to 2 min.

3. The solution of this problem is achieved by the development of the inhibitory after-effect following each positive trial and lasting at least up to the next trial, and by canceling this inhibitory after-effect when the negative trial is over.

The author is graetly indebted to Professor J. Konorski for his valuable suggestions and comments.

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URINARY BLADDER FUNCTION IN EXPERIMENTALLY PRODUCED INTRACRANIAL HYPERTENSION

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It is commonly known that abnormally increased intracranial pressure (ICP) may produce, sometimes, severe functional abnormalities. They include:

1. Central nervous system disorders (headaches, disturbances of awareness and reflexes, abnormalities in EEG).
2. Cardiorespiratory disorders (rise in systemic blood pressure, tachycardia followed by bradycardia, abnormalities in EKG, alterations in respiratory rhythm and amplitude, apnoe).
3. Visual and hearing disorders (decrease in vision acuity, limitation of visual field, papilledema, optic nerve atrophy, decrease of hearing, tinnitus, vertigo).
4. Digestive disorders (nausea, vomiting, abdominal pain, constipation).
5. Muscular disorders (increased or decreased muscular tension and strength).
6. Vegetative (abnormalities in thermoregulation) and humoral disorders.

In recent years, increased intracranial pressure was incriminated to play some, if not decisive role, in the development of hyperacidosis and ulcer of the stomach (D a v i s 1960) as well as some urinary tract disturbances. S a l k and W e i n s t e i n (1939) found experimentally that any greater rises in ICP were followed by a definite decrease or arrest of renal secretion (oliguria or anuria). This was thought to be due to a marked constriction of renal vessels resulting from stimulation of the vasomotor centre. This vasoconstriction was so severe that could not be

compensated by the simultaneously elevated blood pressure. Tönnis (1959), and Tönnis and Bischoff (1961) made an critical analysis of urinary bladder disorders in a large series of patients with brain tumors before and after neurosurgical operations. They found that vesical disorders were frequently associated with intracranial hypertension and rather rarely were due to the presence or location of the tumor itself. This clinical association of intracranial hypertension and urinary bladder disorders has led them to assume that there must be a causative relation between these two conditions. They stated: "*Wir müssen dem vergrösserten intracraniellen Druck einen genetischen Faktor der zentralen Blasenstörung zuerkennen*", and "*Sicher spielt der Hirndruck in der Genese der zentralen Blasenstörung auch eine Rolle*".

Analysis of patients with cerebral tumors observed in the Department of Neurosurgery of the Army Medical Academy at Łódź had shown that intracranial hypertension was associated with disordered urinary bladder function in approximately 50 per cent of patients. It is not known, however, whether this coincidence is casual since in the remaining 50 per cent of patients who displayed vesical disorders cerebrospinal fluid pressure was not increased.

The experiments to be reported were undertaken to ascertain whether intracranial hypertension without any underlying space occupying lesion of the brain would have an effect on urinary bladder function. The problem is complicated and can not be solved on the basis of a clinical study alone due to difficulties in distinguishing what effects should be ascribed to increased ICP and what to the presence of cerebral tumor itself. In addition, there are number of other factors which in brain tumor patients' may modify the urinary bladder function. Therefore experimentation under controlled conditions seems to be essential to the finding of an answer on the question whether or not the vesical disorders are dependent on the generalized increase in ICP. Since in the literature the experimental data were not available it was hoped that such a study would provide data which might secure clearer understanding of the mechanism of vesical disorders in patients with brain tumors.

The basic plan of the study incorporated the following sequence of events:

1. Preparation of animals to cystometric studies of the urinary bladder (first operation),
2. Waiting period during which the bladder function was studied,
3. Induction of intracranial hypertension (second operation),
4. Second period of cystometric studies.

Sufficient time was permitted to elapse between the two operative procedures.

MATERIAL AND METHOD

Seven mongrel dogs unselected as to age, weighing from 12 to 16 kg. were used.

First operation. Preparation of the dog to cystometric studies. The left kidney was exposed and after dissecting of the renal pelvis removed. The left ureter together with renal pelvis was implanted into the skin through a separate stab wound placed somewhat above the main operative incision. On the next postoperative day or few days later when healing was achieved the catheterizations of the bladder via the implanted "ureter-pelvis" and cystometric examinations were started.

Second operation. Induction of the intracranial hypertension. Six main veins in the neck (internal and external jugular, and vertebral veins) were ligated and transected.

Several cystometric studies were made on each dog prior and following the induction of intracranial hypertension. All studies were performed with a simple water manometer without anesthesia in full co-operation of the animal so that not only volume pressure curve but also vesical sensation could be noted.

The technic of both operative procedures and cystometric examinations were described in details and discussed elsewhere (Cieśliński 1964, 1965).

RESULTS

Cystometric studies prior to induction of intracranial hypertension. The ureter was transplanted to the skin 26 to 132 days prior to the second operation. All animals tolerated the operation well and the implanted "ureter-pelvis" healed satisfactorily. In three dogs (Nos. 1, 2 and 5) the volume pressure curves were flat, slowly rising and the vesical capacity amounted 500 to 600 cc. In two dogs (Nos. 4 and 6) the volume pressure curves initially flat ascended more steeply in final stages of bladder filling the vesical capacity equalling 500 to 600 cc. too. In one dog (No. 3) the volume pressure curves were evidently hypertonic, i.e., rapidly and steeply ascending, the vesical capacity being, however, large too (500 cc.). In one dog (No. 7) marked hypertonicity of detrusor was noted in conjunction with hypocapacity (200 to 250 cc.). All the cystometrograms were similar and comparable on successive determinations.

Intracranial hypertension. The operation of venous ligations in the neck was hoped to result in lasting disturbances of the venous outflow from the brain. It was followed by prompt and satisfactory recovery. All animals appeared healthy and behaved normally until the time of autopsy except dog No. 7 whose clinical status progressively worsened. In four animals (dogs Nos. 1, 2, 4 and 7) early, marked (to 4 dioptres) bilateral papilledema developed. It persisted, varying in small ranges only, throughout the period of observation. Slight (0.5 dioptre) unilateral papilledema was present in one dog (No. 3). In two other animals the ocular fundi were within normal limits. Cerebrospinal fluid pressure mea-

sured in the cisterna magna in no instance surpassed 300 mm. of water (maximum 270) slowly decreased with time and in some animals gradually returned to normal levels toward the end of the study. Considerable rise of more than 100 per cent above the initial pressure was noted in three animals (dogs Nos. 1, 3 and 6). At autopsy brain swelling was found in six and encephalomeylomeningitis in one dog. The severity of cerebral swelling varied for the animals were sacrificed at different stages of involvement. It was, however, most marked and widespread (honeycombed appearance of the white matter) in animals that developed the most definite ocular changes, i.e. papilledema.

Cystometric studies following the induction of intracranial hypertension. The animals were examined cystometrically every few days within a long space of time (31 to 105 days) until they were sacrificed. A total of about 120 cystometric examinations were done (from 8 to 26 in each animal). In six animals, any alterations in the cystometrograms, i.e., in bladder response to filling and stretching were characteristically absent in comparison to preoperative studies. Motor and sensory functions of the urinary bladder were not disturbed by increased ICP. In one animal (dog No. 7), despite that his general state and weight diminished the vesical capacity increased and the intravesical pressures lowered definitely. His preoperative volume pressure curves were short and high (low capacity, high pressure) while the postoperative ones became similar to those obtained in other normal dogs. It is possible that undiagnosed cerebral disease may account for changes of cystometrograms preoperatively (hypertonicity) and that the progress of the disease independently or under influence of the venous occlusions altered the bladder response to filling in opposite direction (pronness to hypotonia).

COMMENT

It may theoretically be supposed that intracranial hypertension:

1. Exerts no effect on urinary bladder brain centers and does not interfere with bladder function at all.

2. Has some, limited influence on the cortical and/or subcortical urinary bladder centers thereby altering their function. Full compensation in the dog, however, takes place, for the lower, spinal centers are capable to assure the undisturbed vesical function.

3. Disorders the bladder function only when it is excessively high and prolonged.

4. Influences the bladder function only in conjunction with other local factors, e.g., cerebral tumor (D a v i s 1960).

The present investigation gives clear evidence that intracranial hypertension produced in dogs by means of occlusion of the main venous blood return channels in the neck causes no alterations in the cystometrograms, i.e., in urinary bladder function.

Two objections may arise in the present study:

1. The question fo the transposition of the experimental data to man which is a moot point as in all animal investigations.

2. The question of the adequacy of the experimental model used.

It was shown experimentally that signs and symptoms related to increased ICP generally became manifest when the ICP was raised to values close to the systemic blood pressure or even higher. Less marked intracranial hypertension, however, may also produce some symptoms. Rise of cerebrospinal fluid pressure to 50 mm of mercury (545 mm of water) was followed by ischemia of the brain (Noel and Schneider quoted by Tönnis 1959) and by restlessness, hypokinesis, apathy, headaches, bradycardia, tachypnoe, nystagmus, vomiting (Tönnis 1959, Jennett and Stern 1960, Jennett 1961).

In man, such distinct elevations of ICP (as those produced in animals) are clinically observed when the signs and symptoms of intracranial hypertension develop. There are no absolute values of chronically persisting intracranial hypertension which give rise to clinical manifestations. It was found that in presence of normal blood pressure (120—70 mm of mercury) the cerebrospinal fluid pressure of 280 mm of water could be tolerated without any appreciable signs or discomfort in man (Wolff quoted by Tönnis 1959) as well as in dogs (Clark and Einspruch 1962). On the other hand, it is not known how long should the moderately increased ICP persist to evoke functional disorders. Jennett (1961) believes that such disorders are produced by longstanding (months) intracranial hypertension with brain stem compression.

Bozza et al. (1961) groups the patients with brain tumors as follows:

1. Patients without any clinical or radiological signs of increased ICP,

2. Patients with moderately elevated pressure,

3. Patients with markedly elevated intracranial pressure but without disturbances of consciousness,

4. Patients with disturbances of consciousness (decompensated intracranial hypertension).

According to this classification, the dogs examined are reminiscent of groups 2 and 3 patients. The intracranial hypertension seemed to be sufficiently severe and protracted to allow comparisons with clinical ma-

terial of neurosurgical patients and to conclude that moderate even prolonged intracranial hypertension associated with brain swelling and papilledema does not disorder the urinary bladder functions.

SUMMARY AND CONCLUSIONS

The present work was undertaken to substantiate the suggestion that casual relation between intracranial hypertension and vesical disorders in patients with brain tumors exists. It was found in dogs that cystometrograms were in no way modified by increased intracranial pressure at least under conditions of these experiments. Thus the hypothesis that ICP may induce vesical disorders has not been confirmed. The urinary bladder dysfunctions in patients with brain tumors seem to depend on the factors, the nature of which cannot be yet determined. Further experimental work is necessary to throw more light on this complex problem.

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LIGATION OF SIX MAIN VEINS IN THE NECK AS A METHOD OF PRODUCING BENIGN INTRACRANIAL HYPERTENSION IN DOGS

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The interdependence between passive brain congestion and intracranial hypertension and brain swelling is a clinically and experimentally well established fact.

Compression of the chest, vena cava superior or jugular veins in the neck is followed by a temporary accumulation of the venous blood within the cranial cavity and produces a rise in cerebrospinal fluid pressure (CSF). The pressure promptly returns to normal on release of the compression.

Permanent blocking of the venous return from the entire brain or its parts achieved by means of venous ligations produces intracranial venous engorgment whose degree and durability depends on the calibre of the occluded vein and existence of collateral routes of outflow. This venous congestion may result (if sufficiently severe and extensive) in displacement, increased formation or defective absorption of CSF as well as in dilatation of vessels, slowing of the blood stream, hypoxia and accumulation of the carbon dioxide. Intracranial hypertension, hydrocephalus or brain swelling due to increased vascular permeability may develop.

In human it was stated that:

1. Transverse sinus thrombosis is followed by an increase in intracranial pressure (ICP) and is apparently one of the main causes of a clinical syndrome called pseudotumor cerebri or benign intracranial hypertension.

2. In posttraumatic thrombosis of the superior sagittal sinus the parts of hemispheres drained by its tributary veins were found to be macro- and microscopically edematous and showed minute hemorrhages (Cobb and Hubbard 1929).

3. Jugular veins can be ligated uni- or bilaterally simultaneously or in a two

stage operation. The compensation as a rule takes place by the way of accessory venous outflow channels. Only rarely different degrees of decompensation with transient increase of ICP or distinct clinical signs of venostasis, even resulting in death, occur (Sugarbaker and Wiley 1951, Martin et al. 1951, Dargent 1962).

Experimental studies on occlusion of the channels of exit of the blood from the brain have not been too numerous. The following venous occlusions have been performed:

1. Ligations of external jugular veins (Bedford 1935, 1936, 1937, Müller and Mortillaro 1958, Löblich and Knezevic 1960).
2. Occlusions of dural sinuses (Beck and Russell 1946, Swanson and Fincher 1954, Denny-Brown et al. 1956, Owens et al. 1957, Lemni and Little 1960).
3. Occlusions of cortical veins (Denny-Brown et al. 1956, Owens et al. 1957).
4. Occlusions of the vena cerebri magna (Dandy 1918, Guleke 1930, Bedford 1934, Schlesinger 1940, Bekov 1960).
5. Combined occlusions, e.g.:
   a. occlusion of superior sagittal sinus followed by ligation of ext. jugular veins (Gabryel 1962).
   b. occlusion of both sinuses transversi followed by ligation of ext. jugular veins (Gabryel 1962).
   c. ligation of external and internal jugular veins followed by bilateral occlusion of the condyloid foramen at the base of the skull and by accessory ligation of any superficial veins found in the neck one week later (Bering and Salibi 1959).

They have apparently produced no consistent changes due to the fact that collateral circulation might be sufficient to allow the normal venous outflow, or, that increase in venous pressure might be only temporary or limited to some small areas of the brain. In most experiments only slight, shortliving brain swelling, rise in ICP and, seldom, mild degree of ventricular dilatation developed. Longer lasting alterations were observed by Bekov (1960) after occlusion of the vena cerebri magna (cerebral swelling, hydrocephalus in few animals, often marked elevation of CSF pressure up to 290 to 330 mm of water, that after a fortnight gradually decreased and returned to normal values within 2 to 3 months) and by Bering and Salibi (1959) after combined venous occlusions (see point 5c, a moderate degree of hydrocephalus in 74 per cent of dogs that reached its maximum within 2 to 3 weeks and did not progress, longer lasting considerable but moderate increase of CSF pressure seldom over 200 mm of water not accompanied by brain swelling).

The purpose of this investigation has been to study the effects of major cephalic venous channel occlusions in dogs. The work was undertaken to assess the value of such occlusions in producing chronic cerebral swelling.

MATERIAL AND METHOD

Eleven male mongrel dogs weighing from 6 to 15 kg unselected as to age were used. They were subjected to operation consisting of bilateral ligation of both internal and external veins and one (right vertebral vein complemented after some interval by occlusion of the superior sagittal sinus or bilateral ligation of external, internal jugular veins and vertebral veins. Anesthesia during the operation was achieved with intraperitoneal nembutal 30 mg per kg of body weight. Brains of 3 dogs served as controls.

Operative technique

a) *Occlusion of the veins in the neck.* With the animal placed in the supine position on then operating table the neck was opened by the midline incision. On the left and the on the right external jugular veins were exposed subcutaneously and internal jugular veins in the carotid sheaths. The veins were gently isolated, dissected downward until the venae jugulares communes and their points of entrance into the venae anonymae were visualised. To expose clearly this critical region of confluens venuum lodged behind the clavicle it was in most cases necessary to extend the skin and muscles incision at the root of the neck on both sides of the sternum on a distance of 2 to 3 cm. Wide approach minimized the risk of accidental injury to great arterial or venous vessels or to pleura, enabled to place properly the ligatures on jugular veins and facilitated the exposure of vertebral veins. Vertebral arteries in the region of the sixth cervical vertebra just before they entered the osseous cannal were identified, exposed, freed and retracted apart by a thread, thereby vertebral veins hidden behind the arteries could be approached. After all veins under question were exposed and dissected, ligatures were placed around them. The animal was turned into a right lateral position, the cisterna magna punctured with a spinal needle and CSF pressure recorded (enough time was given to reach a stable level). Then the ligatures were successively tied and all CSF pressure variations observed. The animal was returned on his back, ligatures complemented and the veins transected between them to exclude any possibility of recanalization. Sometimes, 5 to 7 cm long portions of the external and internal jugular veins were resected and main tributaries ligated. Wound was closed by separate sutures in layers. Two rubber drains were left.

b) *Occlusion of the sinus sagittalis superior (SSS).* After trephining a hole aproximately 2 cm in diameter over the midcalvarium the SSS in its posterior portion was exposed and many times ligated by stitching sutures.

Postoperative follow-up

a) *Physical examination.* The animals were observed daily, later periodically. the presence or absence of any signs and symptoms being recorded.

b) *CSF pressure studies.* CSF pressures were registered through the percutaneous cisternal puncture by means of a Claude manometer attached to the needle by a short piece of rubber tubing. Recordings were obtained during operation before and after venous ligations and postoperatively at intervals of 7 to 14 days or more. Care was taken to avoid any loss of the CSF during the procedure. All measurements were performed with the dogs in the right lateral recumbent position on

the flat table with slightly flexed head. With a period of training the dogs became accustomed to the punctures and lay quietly when they were carried out. CSF pressures were taken both under nembutal anesthesia and without anesthesia. No great differences in values were noted.

c) *Ophtalmoscopic studies.* The animal were examined independently by two experienced ophtalmologists with the "Oculus" ophtalmoscope every 3 to 7 days throughout the entire period of survival. The presence or absence of papilledema and appearances of ocular fundi were recorded.

d) *Pathologic studies.* The animals were sacrificed after 4 to 15 weeks with an overdose of nembutal. The brains were removed immediately after death and examined grossly and microscopically. After a craniotomy and opening of both frontal air sinuses the entire vault of the skull was removed with a rongeur. The spinal cord was transected, the brain retracted from behind, both optic nerves at optic chiasma out and after freeing of frontal lobes removed in one piece from the skull. While removing the brain note was made concerning the appearance of the brain surface, congestion and the amount of fluid in the subarachoid space. Both eyes together with the optic nerves were dissected out. Brains were fixed in 4 per cent formalin solution for 10 to 12 days. Multiple horizontal sections of the cerebral hemispheres and cerebellum were made, embedded in paraffin, stained with hematoxylin and eosin and studied microscopically.

e) *Phlebographic studies.* Venographies were done in life as well as after death to determine the channels for collateral blood flow. When the animals were alive the radioopaque medium was injected bilaterally into the ligated stumps of external jugular veins percutaneously or after surgical exposure under local anesthesia. Post mortem, after the brain was removed, the contrast medium was introduced through the sinus petrosus superior uni- or bilaterally, as rapidly as possible. Ten to 20 cc. of 60 per cent Urografin were used. Films were taken in the supine position after almost all the contrast was injected.

RESULTS

The operation is not technically difficult and offers no special problems provided the surgeon well understands the anatomy of the venous system in the neck.

In 3 dogs (group 1), to the bilateral ligation of external and internal jugular veins only unilateral occlusion of vertebral vein was added. One animal died on the first postoperative day. The two others were subjected to subsequent occlusion of superior sinus sagittalis after four weeks following the first operation (Dogs Nos. 2 and 3).

In 8 animals (group 2), both external and internal jugular veins as well as both vertebral veins were ligated. In 3 of them, this type of ligation was complemented by partial excision of the external jugular veins up to facial vein including all the main branches (Dogs Nos. 4 to 11). All animals survived.

Surgical accidents were encountered in 3 cases of the present series. In one dog (that died) a branch of cervical plexus was sectioned with sub-

sequent paresis of the left forelimb. In the second, the thoracic duct while clearing the areolar tissue around the lower end of the left jugular vein was damaged; it was ligated together with the vein with no sequelae (no subsequent leakage of chyle). In the third, a left subclavian artery was temporarily clamped when massive bleeding of one of its branches occurred; transient claudication resulted. Operative complications decreased with knowledge how to do ligations.

No special postoperative care was provided. The outcome was satisfactory. All animals, except the one that died, tolerated the procedure well. They recovered and improved rapidly, were well in every way and behaved normally. No physically demostrable abnormalities developed. No definite physical manifestations of the impaired venous return apart from transitory (2 to 4 days) subcutaneous edema of the neck and mouth especially following the occlusion of the superior sagittal sinus were present. Wound drainage was copious and persisted a fortnight or even longer. In one dog there was a suppuration and dehiscence of the wound. Drains were removed at 7-th postoperative day. The animals did not appear to be in any particular trouble even when increased intracisternal pressure was recorded. It was found that in animals of the second group there was an appreciable and sustained rise in CSF pressure immediately after the veins were tied and in the postoperative period. Immediately after ligations the pressure rose from 20 to 130 per cent above the initial pressure. Such rises (Fishman 1953, Clark and Einspruch 1962) can be held for meanigful and considerable. The pressures remained elevated as long as some weeks or slowly returned to nearly normal levels. In general, a tendency to a slow and progressive decrease was noted. In dogs of the group 1, CSF pressure remained nearly unchanged (Table I).

Ophtalmoscopic examinations in dogs of the first group were entirely negative. Both optic discs were normal in outline and colour. The veins were of normal appearance or only slightly dilated.

Out of the dogs of the second group, 4 developed marked papilledema and 3 did not. Papilledema appeared early within the first week and persisted, sometimes, slightly decrasing throughout the period of observation. The degree of papilledema ranged between 0,5 to 4 dioptres. The appearances of both discs were essentially similar but papilledema was usually more clearly pronounced in one eye. The chocked discs were associated with definite engorgment of veins and progressively increasing pallor (most marked in dog. No. 4 that was longest observed) and blurring of discs outlines. No homorrhages were observed within the discs or in the surrounding retina. In no case a definite regression of papilledema was noted during the period of observation.

Table I

CSF pressures prior and following venous ligations.

Dog No.	CSF pressure			Papilledema
	initially	on ligation	later on	
1	—	—	—	—
2	90	120	100—100—100 on days 10 20 30	—
3	80	100	100	—
4	105	170	250—200—140 on days 28 46 102	+++
5	55	110	115—110—140 on days 18 38 74	+—
6	150	230	270 200 on days 11 31	+ + +
7	90	155	230— 80— 75 on days 4 24 54	—
8	85	140	110 on day 17	—
9	65	90	150—120 on days 23 53	—
10	100	230	200 on day 21	+ + +
11	65	120	100— 80 on days 20 49	+ +

In one dog (No. 5) initially only fullness and tortuosity of retinal veins were observed. This congestion increased with time, and temporal parts and margins of the discs became blurred. The examination on the 67-th day revealed slight papilledema in the right eye, measuring about 0,5 D. (Table II).

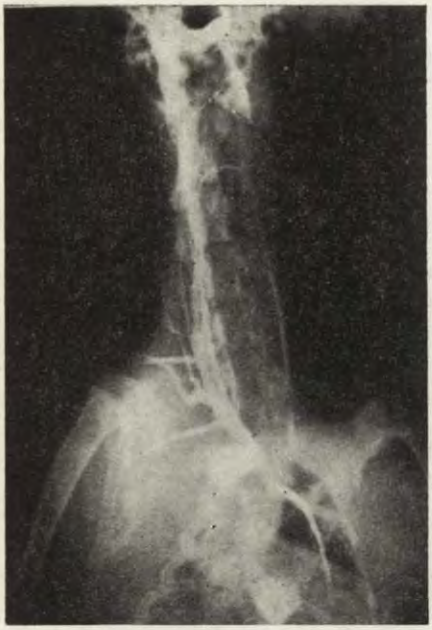

Fig. 1. Normal venography. The contrast medium injected into the sinus petrosus sup. dex. fills on the right side the external, internal and common jugular, and vertebral veins with its main tributaries and on the left side only the external jugular vein. The contrast passes freely into the heart.

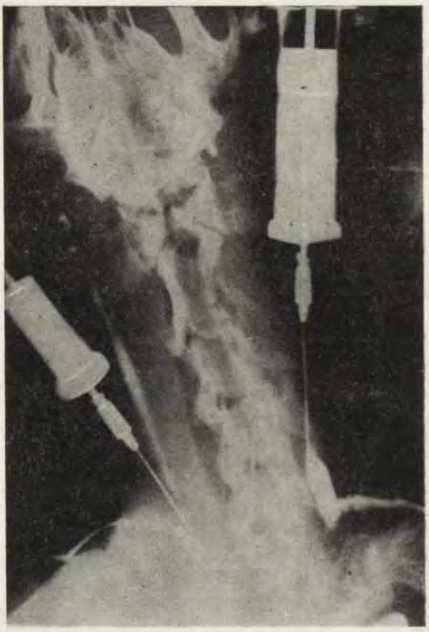

Fig. 2. The opaque medium injected into both jugular veins just above the site of ligation. A retrograde flow through a subscapular veins is clearly visible.

In dogs that had no papilledema the appearances of the optic fundi were normal. Except transient congestion of the veins no alterations were discovered.

The papilledema developed in animals in which most evident and sustained rises in ICP were noted. The CSF pressures were, however, considerably lesser than the appearances of the fundi have led one to suggest. The dogs seemed to have no symptoms referable to papilledema. Gross impairment of vision has not been observed.

Venographies showed that the major venous channels drainage routes in the neck were occluded. Sometimes, the tied jugular veins were found to be dilated in circumference. Retrograde blood flow took place through the external jugular veins tributaries. Anastomotic channels developed around the site of ligation by enlargment of numerous small vessels in the neck (Figs. 1 to 5).

The dogs were observed for a period of time, ranging from 28 to 105 days (Table III).

Table II

The degree of papilledema after venous ligations.

Dog No.	Presence of papilledema	Degree of papilledema
1,2,3	absent	
7,8,9	absent	
4	marked +++	2 to 3D — 7, 18, 25, 32, 39 day 3 to 4D — 46, 56, 60, 66, 79 day 2 to 3D — 105 day
6	marked +++	1,5 to 2D — 4,11 day 2 to 3D — 24, 31, 38 day
10	marked +++	2 to 3D — 8, 19 day 2D — 27 day
11	definite ++	1 to 2,5D — 7 day 0,5 to 1 D — 18 day unmeasurable — 26 day 1 to 2D — 49 day
5	slight +—	in late stages of the observation — 0,5D

Table III

Time of surrival, the degree of brain swelling and papilledema.

Dog. No.	Put to death on day	Brain swelling		Papilledema
		macroscopic	microscopic	
1	1 (died)	—	+	—
2	90 after the 1st operation 63 ,, ,, 2nd ,,	—	+	—
3	67 after the 1st operation 39 ,, ,, 2nd ,,	—	+	—
4	105	+	+++	+++
5	81	—	++	+—
6	41	+	+++	+++
7	80	—	+	—
8	28	—	+	—
9	53	—	+	—
10	31	—	—	+++
11	49	—	++	++

Fig. 3. The opaque medium injected into both external jugular veins visualizes marked distention of these veins and a definite net of small collaterals close to the site of ligation. The retrograde flow through the tributaries of the external veins is clearly visible.

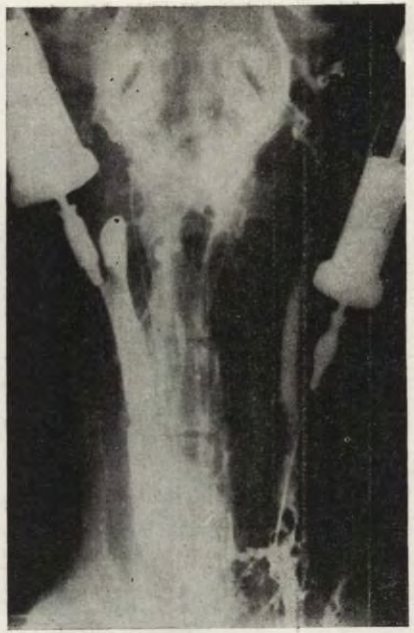

Fig. 4. The opaque medium injected into both external jugular veins visualises marked distention of these veins and a definite net of small collaterals close to the site of ligation. The retrograde flow through the tributaries of the external veins is clearly visible.

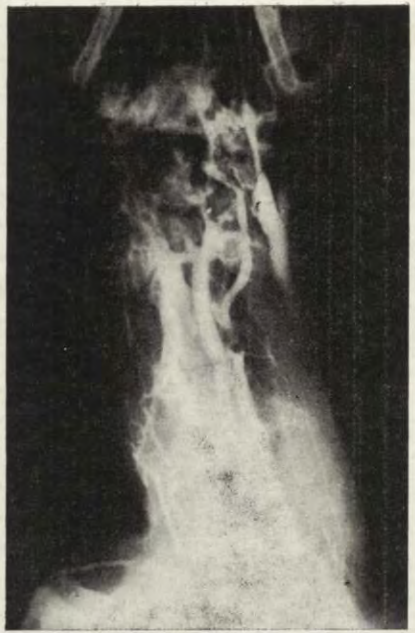

Fig. 5. The contrast medium injected into the sinus petrosus sup. shows definite distention of ligated veins and many collateral routes of venous outflow.

Postmortem findings

Grossly, marked dilatation of the entire venous system of the hemispheres were noted only in two dogs (Nos. 8 and 9). In those who developed most distinct elevations of CSF pressure (Dogs Nos. 4, 6 and 11) and papilledema there was rather marked pallor of the brain. The brains were tense and bulged slightly through the dural defects. In those who had superior sagittal sinus occlusions the dura was adherent to the underlying cortex in the vicinity of the trephine opening. Only in dogs Nos. 4 and 6 some narrowing of sulci and flattening of gyri were noted. In others, the cerebral convolutions appeared normal. In dogs Nos. 4 and 6, somewhat larger amounts of CSF fluid escaped under pressure when the dura was opened. In others, there was very little fluid on the surface of the brain.

Lateral ventricles were apparently normal, symmetrical.

Microscopically, areolar appearance of white matter and dilatation of perivascular spaces in the white and grey matters was present in all (except one) examined brains as well as vascular stasis with multiple mi-

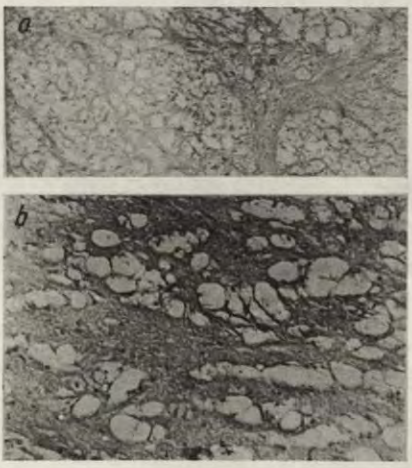

Fig. 6. Microscopic picture of brain swelling. Hematoxylin-eosin stain.

nute diapedesis. These alterations which are held to be the reliable criteria for microscopic diagnosis of cerebral swelling were most severe (definite honeycombed appearance of the white matter) and extensive in dogs which displayed the most marked signs of intracranial hypertension (Dogs Nos. 4, 6 and 11, cf. Fig. 6).

In dog No. 10, no microscopic picture of cerebral swelling was found; intracranial hypertension was due to myelomeningoencephalitis of unknown cause.

COMMENT

The present investigation shows that in dogs ligation of the six main veins in the neck may be followed by definite, sustained alterations. In some animals, no clinical evidence of the impaired venous return was observed but mild degree of cerebral swelling was found histologically. In others, clinical evidence of intracranial hypertension and microscopical evidence of diffuse cerebral swelling were present.

Ligation of five main venous vessels, leaving intact one vertebral vein even complemented by occlusion of superior sagittal sinus produced no clinical signs or symptoms but some degree of brain swelling was manifest at autopsy.

In dogs who had symptoms the picture may be compared to the clinically in human observed syndrome known as pseudotumor cerebri or benign intracranial hypertension (Dandy 1937, Ray and Dunbar 1951, Wagener 1954, Feldman et al. 1955, Foley 1955, Berg et al. 1955, Bradshaw 1956). The most essential features of this syndrome are:

clinically: general wellbeing of the patient with no disturbances of awareness, intellect or vision sometimes associated with headaches, nausea, vomiting; absence of focal neurological signs, increased pressure of CSF and its normal composition, marked, bilateral papilledema.

pathologically: normal appearance of the brain surface in spite of the increased tension of the dura, normal ventricular system with no excess of CSF in the subarachnoid space, cerebral swelling. Absence of the cerebral tumor or space occupying lesion or any other well defined cause to explain the hypertension of CSF.

Though in different patients some differences in clinical picture as well as in the pathology were found (some dilatation of ventricles in later stages of the disease, increased capacity of the subarachnoid space with some excess of CSF) marked papilledema, general wellbeing increased ICP and absence of internal hydrocephalus are held to be the most constant, outstanding and characteristic features.

Some of our animals with impaired venous return showed all these signs (no definite evidence of any general or neurological symptoms marked papilledema, hypertension of CSF, brain swelling in conjunction with undistorted, normal sized ventricles, without excess of fluid on the surface of the brain) thus fullfilling the criteria necessary to diagnose the syndrome of benign intracranial hypertension. Despite the fact that CSF pressure was not markedly elevated, the definite severe degree of papil-

ledema indicated that a marked intracranial hypertension was present. Brain swelling was found only microscopically. But as stated by Prados et al. (1945) "*the increase in the brain bulk can not be accepted as condition sine qua non for the diagnosis of cerebral edema. The volume of brain is increased only when the amount of fluid within the brain is exaggerated. In milder reactions, one sees only the histological picture of edema without much change in the volume of brain.*"

The condition described in this paper should be related to a sufficient degree of venous congestion within the skull and brain due to obstruction of the main channels for the return of venous blood in the neck and permanent partial inadequacy of the collateral routes. Though partially inadequate, the return was sufficient so that no serious impairment of general health developed. The degree of the stasis was, however, extensive enough to induce intracranial hypertension, mild degree of cerebral edema and papilledema. The more complete the venous cephalic drainage occlusion the more prolonged and irreversible syndrome of intracranial hypertension seemed to be obtained. When the collateral, compensatory circulation was fully reestablished, i.e., momentary accomodation took place, no alterations occurred or stasis was transient and negligible.

Collateral pathways of venous outflow from the brain are numerous and well developed. After bilateral ligation of jugular and vertebral veins the venous blood leaves the brain via the auxiliary channels-posterior condyloid, occipital, emissary, ophtalmic veins and through the phyryngeal, pterygoid, oesophagal and vertebral plexuses. The emissary veins piercing the bony wall of the skull are not capable of any appreciable distention. The pterygoid and orbital plexuses as well as the external (surrounding the vertebral arches lying deep in the muscles of the neck and back) and internal vertebral plexuses (occupying the space between the dura and the bony wall of the spinal canal) may distend appreciably and aid significantly the outflow. Vertebral plexuses have a flow potential equalling that of both jugular veins. This high blood carrying power of collateral venous channels was found to be great in man and in dog (Martin et al. 1951, Sugarbaker and Wiley 1951, Mc Clure and Greene 1959). Collateral compensation is however, not so evident in other species and plays in rabbits as well as in rats no significant role (Müller and Mortillaro 1958, Löblich and Knezevic 1960). The increase of diameter of veins could be easily observed in present experiments. On ligation of jugular veins marked distention of vertebral veins occurred. The venous outflow is further facilitated by some anatomical peculiarities of the veins of the head and neck. They anastomose profusely and had no valves so that retrograde flow of venous blood may easily take place (Fig. 2).

When after ligation restoration of the venous circulation is delayed due to the fact that collaterals are defective or temporarily inadequate some congestive signs may be present but they disappear with time.

It should be emphasized that to achieve a complete block of the venous outflow from the cranium very extensive ligations comprising 13 successive operative steps (incompatible with life) were necessary (Mc Clure and Greene 1959).

Apart from venous occlusions several methods have been described to produce experimental intracranial hypertension, hydrocephalus and or brain swelling. Intracranial hypertension, hydrocephalus and brain swelling can be experimentally accomplished by:

1. Subarachnoid injection of isotonic fluids or extradural compression of the brain,
2. Intracisternal or intraventricular injection of isotonic fluids,
3. Intravascular administration of fluids,
4. Intracisternal or intraventricular injection of irritative substances,
5. Mechanical blocking of the CSF circulation routes,
6. Different forms of injury to the brain:
   a) simple exposure,
   b) wounding the brain,
   c) striking the head (cerebral concussion),
   d) cold application.
7. Production of the space occupying lesions,
8. Injection into the brain of some bacterial and toxic agents,
9. Oral ingestion or parenteral administration of certain poisons or drugs,
10. Vitamin A deficient diet,
11. Stimulation of the peripheral nervous system,
12. Producing of general or regional cerebral ischemia or anemia.

The methods of subarachnoid, intracisternal or intraventricular injections of fluid enable producing any desired instantaneous increase in ICP but for a short period of time only.

The methods of intracisternal or intraventricular injections of irritative substances and methods of mechanical blocking of the CSF pressure circulation as well as feeding with vitamin A deficient diet are designed to produce experimental internal hydrocephalus. More or less severe hydrocephalus is associated most often with a moderate increase in ICP. Rarely concomitant brain swelling or papilledema are present. As a rule the hydrocephalic animals can be followed up for a period of months and it depends on the degree of hydrocephalus whether the general status of the animals is disturbed or not.

The remaining methods may serve to study the cerebral swelling. The swelling is, as a rule, transitory and persists hours or days only. It may be generalized (extradural compression, intravascular administration of fluids, simple exposure of the brain, cerebral concussion, space taking

lesions, stimulation of the peripheral nervous system), or, localized, perifocal (cold application, wounding the brain, arterial ligations). The increase in ICP is most often moderate. Distinctly raised ICP (up to 1200 mm of water) and marked papilledema occur within the first hours only after brain lesions produced by cold application.

Prolonged brain swelling may occur after injection of etopalin-kaolin paste into the brain substance or after administration of alkyl tin compounds. The swelling is visible only on microscopic examination and may be slight and localized around the lesion (etopalin-kaolin paste) or severe and diffuse (alkyl tin compounds). This swelling is, however, not associated with papilledema and data are lacking on the CSF pressures.

Most of the heretofore described kinds of venous ligations of the cerebral veins were followed by no or only slight, transient brain swelling and, sometimes, by hydrocephalus and moderate increase of ICP. In any case, after venous ligations papilledema was observed.

Many of above surveyed methods necessitate extensive intracranial manipulations which may result in damage to the brain and give high mortality rate and high percentage of complications and failures. There are still difficulties in producing desired edematous lesions of the brain with regularity. Most of these methods are suitable for acute of short--term studies only.

No such procedure of ligations of the main veins in the neck of the dog and no similar results to the ones presented in this paper have been described.

The presented procedure of producing cerebral swelling is technically simple, permits avoiding any side effects of opening the skull, of brain exposure and leaves the brain undamaged from external violence, local mass or compression. Complications are absent, mortality rate is low, prolonged survival is achieved.

In every instance, there was histological evidence of mild or definite generalized brain swelling and venous engorgment with numerous, small hemorrhagic areas widespread throughout the cerebrum without apparent increase in the brain volume. In part of the animals subjected to operation, the brain swelling was associated with clinical manifestations of chronic intracranial hypertension such as significantly increased CSF pressure and papilledema. It seems that in those animals the inadequacy of the auxiliary venous return routes was present and therefore the compensation of venous blood circulation from the brain was impossible.

Sustained elevations of CSF pressure of approximately 100 per cent or even more above the initial level are to be regarded as considerable though not excessive or incompatible with life. The CSF pressure though elevated was not so high as the degree of papilledema would suggest. This

was in accordance with the observations of Bradshaw (1956), on the benign intracranial hypertension in humans. It was previously shown by Badmaev (1957) and may be confirmed by the present experiments that widespread and distinct cerebral swelling may be evident in the presence of 100 per cent increase of CSF pressure.

Papilledema when present developed as a rule early, being an outstanding clinical symptom and could be observed without much change during a long period of time. Its developing was not prevented by obliteration of perineural spaces or chiasmatic arachnoiditis which are likely to occur in other methods.

Experimental production of benign intracranial hypertension was possible only in part of animals subjected to extensive venous ligations in the neck. The adequacy or inadequacy of the collateral venous channels remaining after ligations and *eo ipso* the final results of such ligations can not be predicted with certainty before operation.

This experimental model seems to be suitable for long term studies on intracranial hypertension. It may be of interest because "*there where we see raised pressure without tumor or hydrocephalus may be found the key to many unsolved problems of intracranial dynamics*" (Foley 1955). The benign intracranial hypertension is a relatively rare syndrome. Its experimental production permits further study and may help in solving problems in patients with brain tumors, e.g., whether some abnormalities in function are dependent on the kind or localization of the tumor or are to be ascribed exclusively to the concomitantly raised intracranial pressure.

SUMMARY AND CONCLUSIONS

This paper presents the results of ligation of six major venous vessels in the neck or 5 major vessels complemented by occlusion of the supperior sagittal sinus in the dog. All (9) animals (except one) revealed at autopsy more or less marked degree of cerebral swelling (loosening of the brain structure, honeycombed appearance of the white matter, distention of perivascular spaces both in the grey and white matter, widespread minute petechial hemorrhages and signs of passive congestion). In some animals, exclusively after ligation of jugular and vertebral veins bilaterally, a clinical syndrome of pseudotumor cerebri (benign intracranial hypertension) developed being manifested by general wellbeing, normal behaviour, moderate increase in the CSF pressure and presence of frank, bilateral papilledema.

No such experimental method of producing benign intracranial hypertension has been heretofore described. In many respects, it may prove sa-

tisfactory to study in chronic experiments the influence of intracranial hypertension on body functions. This method was adopted for long term studies on the relationship between pure (without brain tumor) intracranial hypertension and urinary bladder functions.

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DIE AUSWAHLSCHWELLE, DIE ABWEISSCHWELLE UND DIE GESCHMACKSTOLERANZ VON WASSERLÖSUNGEN DES CHININ-HYDROCHLORIDS, DER ZITRONENSÄURE, DER SACHAROSE UND DES KOCHSALZES EINIGER ARTEN VON INSEKTENFRESSERN UND NAGETIEREN

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Bei Prüfungen der Geschmacksempfindlichkeit der Säugetiere werden meistens die Präferenzmethode und die gustometrische Methode angewandt. Die letztere beruht auf Vermessung der bioelektrischen Aktivität der Nerven, welche im Laufe der Einwirkung verschiedener Substanzen von verschiedener Konzentration auf die Wallpapillen, die Anreize von den Schmeckzellen ausleiten.

Die Präferenzmethode stützt sich auf Verabreichung den Tieren zur Auswahl reines Wasser und Wasser, in dem Geschmackssubstanzen aufgelöst waren. Die Methode gestattet die Feststellung der Auswahl-oder Abweisschwelle, bieziehungsweise die Feststellung der Geschmackstoleranzgrenze bei Testsubstanzlösungen. Wenn im Moment der Empfindung eines Geschmacks das Tier sofort positiv oder negativ, auf die jeweilige Testlösung, reagiert, dann kann im ersten Falle die Auswahlschwelle und im zweiten die Abweisschwelle bestimmt werden. Laut der Suggestion von P a t t e n und R u c h (1944) sollen diese Schwellen an die Geschmacksschwellen angrenzen. Es kommt auch vor, dass das Tier,

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obgleich es den Geschmack verschiedener Substanzen empfindet, sich ihnen gegenüber bei kleinen Konzentrationen gleichgültig verhält, und erst bei starken Konzentrationen beginnt die Abweisreaktion. Diese Art von Reaktion auf die Lösung der Geschmackssubstanz, deren Verzehrung auf die Hälfte der getrunkenen Menge reines Wassers fällt, bestimmt die Geschmackstoleranzgrenze. Es gibt noch eine vierte Möglichkeit, wenn das Tier an der Grenze der Geschmacksschwelle auf die jeweilige Substanz positiv und bei ihrer starkeren Konzentration, negativ reagiert. Bei dieser Erscheinung kann sowohl die Auswahlschwelle als auch die Schwelle der Geschmacktoleranz bestimmt werden. Als Auswahlschwelle wurde nach W e d e l l (1936) eine solche Lösung der jeweiligen Substanz angenommen, derer getrunkene Dosis doppelt so gross zu sein pflegt, als die in derselben Zeit verzehrte Wassergabe. Bei Umwendung dieser Erscheinung wurde die erreichte Schwelle Abweisschwelle genannt.

Der erste Teil dieser Arbeit wurde am Lehrstuhl für Zoologie der Hochschule für Landwirtschaftskunde (S.G.G.W.) im Jahre 1960/61 ausgeführt. Man bestimmte die Schwelle des Abweises der Wasserlösungen des Chininhydrochlorids durch Maulwürfe. Es wurden daselbst Versuche durchgeführt über die Schwelle der Auswahl des Maulwurfes auf Sacharose, Zitronensäure und Kochsalz. Die Bestimmung dieser Schwelle mit der Präferenzmethode erwies sich als unausführbar. Die Tiere reagierten nicht auf die Schwellenwerte der Testlösungen. Man befasste sich in einer anderen Arbeit (C h r z a n o w s k i 1962) mit der Bestimmung der Grenze der Geschmackstoleranz des Maulwurfs auf die obegenannten Substanzen, bei Anwendung der Methode einer Entziehung von reinem Trinkwasser dem Tier. Ein weiterer Teil dieser Arbeit betrifft Prüfungen über die Abweisschwelle, die Auswahlschwelle und die Grenze der Geschmackstoleranz bei der Waldrötelmaus (*Clethrionomys glareolus* S c h r e b.), dem Degu (*Octodon degus* M o l.), bei der Hausspitzmaus (*Crocidura russula* H e r m.), und der Feld-Waldmaus (*Apodemus sylvaticus* L.). Diese auf der Auswahlmethode sich stützende Prüfungen wurden im Jahre 1961/62 im Zoologischen Institut der Goethe-Universität in Frankfurt/Main durchgeführt.

Mit Ausnahme der Hausspitzmäuse befand sich jedes der Versuchtiere in einem besonderen Käfig. Die obengenannten Spitzmäuse hielt man gemeinsam, wegen geringer Mengen der durch sie getrunkenen Flüssigkeit, in einer kleinen Herde. Die Maulwürfe, wurden mit Pferdefleisch gefüttert. Das Futter der Waldrötelmaus, der Feld-Waldmaus und der Art Degu bestand aus Standardfutter, Erdnüssen, Sommerblumensamen, Apfelschalen, Löwenzahnblätter und Salat. Die Hausspitzmäuse wurden mit Larven des Mehlkäfers halb zu halb mit Rindfleisch vermengt, gefüttert. Alle Tiere wurden mit Hilfe von Tränkgefässen (zwei je Käfig) getränkt, die in gleicher Höhe an beiden Seiten des Käfigs in gleicher Entfernung von der Lagerstätte untergebracht waren. Die Tränkgefässe wurden einmal täglich gewaschen, mit frisch zubereitetem Gehalt gefüllt, das linke auf das rechte ausgewechselt; man bemühte sich alle Vorsichtsmassregeln zu wahren, um die Bevorzugung eines der Gefässe durch die Tiere zu vermeiden. Die Tränkgefässe waren aus Absorptionsröhrchen ausgeführt. Anfänglich verabreichte man während 16—20 Tagen in beiden Gefässen reines Wasser, bis zum Augenblick als die Wasserentnahme aus beiden Gefässen ungefähr ausgeglichen wurde. Dann begann das Experimentieren. Man

gab den Maulwürfen in einem der Tränkgefässen Testsubstanzen verdünnt mit Wasser aus der Wasserleitung, und im anderen, Wasserleitungswasser. Den übrigen Tieren gab man statt des Wasserleitungswassers destiliertes Wasser. Diese Neuerung wurde deswegen eingeführt, weil das Frankfurter Wasserleitungswasser stark (stärker als in Warschau) chlorig war, und hätte, des Geruchs oder Geschmacks wegen, die Ergebnisse des Versuches beeinflussen können.

Die Messung des Umfanges der in Tagesabständen durch die Tiere getrunkenen Flüssigkeitsmengen wurde mit einer Genauigkeit bis 0.5 cm^3 ausgeführt.

Auf die Messungen der Schwellen gestützt, die für jedes einzelne Tier gesondert bestimmt wurden, wurden die Verlässigkeitsintervalle für die Art verfertigt. Zur Bestimmung der Verlässigkeitsintervalle bediente man sich der Anordnung von t-Student bei einem Koeffizienten 0.95. Dieser Koeffizient sieht die Möglichkeit von 5 Irrtümern auf 100 untersuchte Fälle vor. In dieser Art von Versuchen, wie die meinigen, ist die Genauigkeit der Messung bei Berücksichtigung des Koeffizienten 0.95 als hinreichend angesehen (F i s c h e r 1949).

Infolge der Haltung der Hausspitzmäuse in Herden, konnten die Zuverlässigkeitsinterwalle dieser Tiere nicht festgestellt werden.

I

Prüfung der Geschmacksempfindlichkeit des Maulwurfs (*Talpa europea* L.), der Hausspitzmaus (*Crocidura russula* H e r m.), des Degu (*Octodon degus* M o l.) und der Waldrötelmaus (*Clethrionomys glareolus* S c h r e b.) auf Wasserlösungen des Chininhydrochlorids.

Man gebrauchte zu den Prüfungen 10 Maulwürfe, je acht Tiere des Degu und der Waldrötelmaus, sowie fünf Hausspitzmäuse. In der Versuchsperiode mit Chinin wurden aus dem Futter der Nagetiere die Blätter des Löwenzahnes, wegen seines bitterlichen Geschmackes, der die Empfindlichkeit der Tiere auf Chinin vermindern konnte, ausgeschlossen.

Die erste, den Maulwürfen verabreichte Testlösung war eine Lösung mit einer möglichst niedrigen, jedoch so hohen Konzentration, dass sie sogar durch sehr durstige Maulwürfe ohne irgendeiner anderen Trinkmöglichkeit nicht getrunken wird. Das Experimentieren mit den verbleibenen Tieren begann mit einer verhältnismässig viel schwächer konzentrierten Lösung und zwar ab einer 0.064 g/100 ml. betragenden Verdünnung des Chininhydrochlorids. Nachher verabreichte man den Versuchsobjekten immer schwächere Chininlösung (wobei die vorhergehende Lösung immer doppelt so stark war, als die nachfolgende) einschliesslich bis zu den vorschwelligen Lösungen. Der Übergang von den stark konzentrierten Lösungen zu den schwachen, wurde nach P a t t o n und R u c h (1944) angenommen. Begründet war dies dadurch, dass die umgekehrte Reihenfolge der verabreichten Verdünnungen eine Abstumpfung der Reaktion der Tiere auf Chinin verursachen und dadurch die Abweisschwelle erhöhen konnte. Dieselbe Chininkonzentration wurde während zwei einander nach folgenden Tagen abwechselnd einmal in einem, das zweite Mal im anderen Tränkgefäss verabreicht (woraus die durchschnittliche Tagesverzehrung berechnet wurde). Dies hatte als Zweck die eventuelle Bedeutung der (rechts oder linksseitigen) Lage des Gefässes auszuschalten. Die Ergebnisse illustriert die Zusammenstellung 1.

Die Abweisschwellen-Streuung (oder Toleranzgrenze?) ist beim Degu sehr gross; deswegen ist das Verlässigkeitsintervall sehr breit, und es

Zusammenstellung 1

Art	Die Auseinanderstellung der Abweisschwellen in g/100 ml	Die durchschnittliche Abweisschwelle in g/100 ml	Der Verlässigkeitsintervall in g/100 ml
Degu	0.00047 (Toleranzgrenze?) 0.048	0.0144 (Toleranzgrenze?)	—
Waldrötelmaus	0.0000487 0.001	0.000368	0.000101 0.000635
Hausspitzmaus	—	0.00021	—
Maulwurf	0.0000049 0.0000531	0.0000199	0.0000109 0.0000363

wäre unzweckmässig ihn hier anzugeben. Aus obiger Zusammenstellung kann man aber (auf der Unverbundenheit der Verlässigkeitsintervalle der genannten Arten sich stützend) den Schluss ziehen, dass am empfindlichsten auf Chininchlorid die Maulwürfe und erst nachher die Hausspitzmäuse, die Waldrötelmäuse und die Degu sind. Bei einigen Exemplaren des Degu konnte bei Chininkonzentrationen, die niedriger als die Grenzkonzentrationen waren, eine grössere Ausnahme der Testlösung als

Ta

Talpa europaea L.

Tägliche Flüssigkeits

Konzentration des Chininhydrochlorids in g/100 ml	A		B		C		D	
	a	b	a	b	a	b	a	b
4×10^{-3}	1.5	9.5	4.0	18.0	1.0	19.0	1.0	12.0
2×10^{-3}	2.0	11.5	3.5	10.5	2.5	17.0	1.0	15.5
10^{-3}	1.5	12.0	6.5	30.0	1.0	16.5	1.0	12.5
5×10^{-4}	2.0	9.5	1.0	19.0	1.0	25.0	1.5	13.5
$5^2 \times 10^{-5}$	1.0	12.5	1.5	21.0	1.5	29.0	1.0	15.5
$5^3 \times 10^{-6}$	1.5	18.0	4.5	22.0	3.0	28.0	4.5	10.0
$5^4 \times 10^{-7}$	3.0	12.5	4.0	22.0	1.5	11.0	4.5	10.5
$5^5 \times 10^{-8}$	2.0	5.5	4.5	11.0	7.0	6.5	5.5	6.5
$5^6 \times 10^{-9}$	3.0	5.5	4.5	12.0	6.5	11.0	3.0	8.0
$5^7 \times 10^{-10}$	4.5	7.0	5.0	7.5	7.0	8.0	7.0	8.5
$5^8 \times 10^{-11}$	7.0	6.5	4.5	4.0	6.0	5.5	5.5	9.5
$5^9 \times 10^{-12}$	5.0	3.0	4.0	3.5	—	—	6.0	7.0

a Wasser mit Chininhydrochlorid
b Wasser aus der Wasserleitung

des Wassers beobachtet werden. Dies konnte davon zeugen, dass diese Exemplare den bitterlichen Geschmack der Flüssigkeit (genauer gesagt: den Geschmack von stärker verdünntem Chinin) dem geschmackslosen oder fast geschmacklosen destillierten Wasser vorziehen (Baldwin et al. 1959, Zotterman 1956). Da diese Erscheinung nicht bei allen Einzelwesen auftrat, und bei denen sie erfolgte schwerlich eine Regelmessigkeit ergründet werden könnte, kann die hier und dort auftretende Präferenz der Testlösung als zufällig angesehen werden, und dies umsomehr, da die Degu-Exemplare unter allen Versuchstieren das am wenigsten augenglichene Trinken aus beiden Gefässen aufwiesen.

Bell (1959a, b) gibt bekannt, dass die Ziegen vor Beginn einer Ablehnung von stärker konzentrierten Chininlösungen die schwächeren Konzentrationen dem Wasser vorzogen. Dies deutet darauf hin, dass die durch Bell bestimmte Schwelle die Toleranzgrenze dieser Tiere bei der Chinindihydrochloridlösungen bildet.

Niedriger als der Ziegen, aber verhältnismässig noch stark konzentrierte Grenzwerte der durch die Makake und Degu abgelehnten Chininlösungen scheinen ebenfalls die Geschmackstoleranzgrenze dieser Tiere nud nicht ihre Abweisschwelle zu bestimmen. Diese Voraussetzung wird durch die Tatsache veranlasst, dass die Grenzwerte der Makake und der Degu viel höher sind, als die Werte der für den Menschen bestimmten Geschmacksschwelle auf Chinin.

belle I

verzehrung in cm^3

E		F		G		H		I		J	
a	b	a	b	a	b	a	b	a	b	a	b
1.0	12.0	1.0	10.5	1.5	8.0	1.5	14.5	1.0	19.0	2.0	21.0
1.0	13.0	2.0	18.0	2.5	8.0	1.5	13.0	1.0	19.0	1.5	19.0
1.0	13.5	1.5	20.5	3.0	10.0	1.0	17.0	1.5	22.0	2.0	17.5
2.0	19.5	1.5	23.0	3.0	10.5	1.0	16.0	2.0	29.0	2.5	17.0
1.0	15.0	4.0	24.5	2.0	7.5	1.5	24.0	5.0	22.5	2.0	29.0
0.5	4.5	2.5	25.0	3.0	10.0	1.5	23.0	7.5	15.5	10.0	32.5
3.0	23.5	2.5	27.5	3.0	15.5	3.0	17.5	9.0	18.0	9.0	19.0
4.0	10.5	1.0	18.0	16.0	12.0	6.0	14.0	4.5	17.5	12.5	9.0
4.0	7.0	5.5	20.0	—	—	2.0	11.0	5.5	9.5	21.5	17.0
5.0	8.0	7.0	17.5	—	—	3.5	4.5	7.5	10.0	2.5	12.0
2.5	3.5	11.0	13.0	—	—	4.0	2.0	6.5	8.0	—	—
5.5	4.0	11.0	14.0	—	—	—	—	5.0	9.5	—	—

Man dürfte einige Säugetiere folgendermassen ordnungsmässig nach der Höhe ihrer durchschnittlichen Abweisschwelle, beziehungsweise der Toleranzgrenze der Chininhydrochlorid- und Chinindihydrochloridlösungen (bezeichnet durch ein *) aufstellen:

Zusammenstellung 2

Art	Die durchschnittliche Abweisschwelle in g/100 ml.	Verfasser
Ziege	0.125* = Toleranzgrenze?	Bell 1959
Makak	0.025 = ,,	Patton und Ruch 1944
Degu	0.0144 = ,,	
Schimpanse	0.0065	Patton und Ruch, 1944
Kalb	0.00385*	Bell, 1959 a, b
Mensch	0.0025 = Geschmacksschwelle	Engel (nach Patton und Ruch 1944)
Ochs	0.0019*	Bell und Williams 1959
Waldrötelmaus	0.000368	
Albino Ratte	0.0003	Patton und Ruch 1944
Hausspitzmaus	0.00021	
Maulwurf	0.0000199	

Tabelle II

Crocidura russula Herm.

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration des Chininhydrochlorids in g/100 ml	A+B+C+D+E	
	Wasser	
	mit Chininhydrochlorid	destilliert
$2^3 \times 10^{-3}$	0.5	4.0
$2^2 \times 10^{-3}$	0.5	5.5
2×10^{-3}	0.5	5.0
10^{-3}	1.0	5.0
5×10^{-4}	1.0	5.5
$5^2 \times 10^{-5}$	2.0	5.0
$5^3 \times 10^{-6}$	4.0	5.0
$5^4 \times 10^{-7}$	3.0	2.5
$5^5 \times 10^{-8}$	3.0	2.0

Tabelle III

Octodon degus Mol.

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration des Chininhydrochlorids in g/100 ml.	A		B		C		D		E		F		G		H	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
$2^6.10^{-3}$	2.0	9.5		14.0	0.5	5.0	0.5	1.5	8.0	19.0	1.0	6.0	0.0	1.5	7.0	24.0
$2^5.10^{-3}$	2.0	15.0	7.0	14.5	0.5	9.0	1.0	1.5	3.5	13.5	1.5	8.5	1.0	2.0	6.0	16.0
$2^4.10^{-3}$	3.5	18.0	7.5	14.5	1.0	6.0	1.5	2.0	1.5	4.5	0.5	1.0	0.5	3.0	3.0	6.0
$2^3.10^{-3}$	12.5	14.0	13.5	8.0	1.0	9.0	1.0	2.5	5.0	13.5	1.0	6.0	3.0	3.0	8.5	2.5
$2^2.10^{-3}$	4.5	29.5	13.0	10.0	2.0	8.0	1.0	3.0	6.0	12.5	2.0	2.5	6.5	6.5	11.0	8.5
$2 .10^{-3}$	17.0	10.0	13.5	9.5	0.5	3.0	0.5	1.5	5.5	7.0	3.0	2.0	3.5	3.5	10.0	7.0
10^{-3}	13.5	8.0	9.5	9.5	1.0	5.5	1.5	11.0	14.0	13.5	4.0	4.0	3.5	3.5	6.0	11.0
$5 .10^{-4}$	14.5	13.5	13.5	9.5	1.0	6.0	2.0	3.0	3.0	4.0	4.5	1.5	4.0	4.0	10.0	3.5
$5^2.10^{-5}$	13.5	3.5	11.5	13.0	5.0	1.5	3.0	1.5	7.5	8.0	4.5	3.5	5.5	5.5	1.5	13.0
$5^3.10^{-6}$	16.0	2.0	7.0	8.0	1.5	1.0	7.5	2.0	2.5	6.0	2.5	1.0	1.0	1.0	3.5	6.0
$5^4.10^{-7}$	12.0	7.5	19.5	8.5	7.0	4.0	2.0	1.5	9.0	13.5	1.0	1.5	3.0	3.0	1.5	11.5

a Wasser mit Chininhydrochlorid
b Destilliert

Tabelle IV

Clethrionomys glareolus Schreb.

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration des Chininhydrochlorids in g/100 ml.	A		B		C		D		E		F		G		H	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
$2^6.10^{-3}$	0.5	4.0	0.5	6.0	0.5	7.0	0.0	4.0	0.5	3.5	0.5	3.0	1.0	9.0	0.5	3.5
$2^5.10^{-3}$	0.0	3.5	1.0	11.0	0.5	6.0	0.0	4.0	0.5	3.5	0.5	3.0	1.5	13.0	0.0	4.0
$2^4.10^{-3}$	0.5	5.0	1.0	6.0	1.0	5.0	0.0	4.5	0.5	3.5	0.5	3.5	1.0	9.0	0.0	4.0
$2^3.10^{-3}$	1.0	4.5	1.5	10.0	0.5	5.0	0.5	3.0	0.5	3.5	0.5	3.5	0.5	13.5	0.5	4.5
$2^2.10^{-3}$	1.5	5.5	1.5	10.0	1.0	4.0	0.5	3.5	0.5	3.5	0.5	4.0	1.0	13.5	0.5	3.5
$2 .10^{-3}$	1.0	4.5	1.5	8.0	1.0	4.5	1.0	3.0	0.5	3.0	0.5	2.5	0.5	13.0	1.0	3.0
10^{-3}	2.0	4.0	4.0	10.5	1.5	4.0	0.5	3.0	0.5	3.0	0.5	3.0	1.0	13.5	1.0	3.5
$5 .10^{-4}$	3.0	3.0	5.0	7.0	1.5	4.5	1.5	3.0	1.0	3.0	0.5	3.5	3.0	13.5	1.0	3.0
$5^2.10^{-5}$	3.0	2.0	6.0	5.0	2.5	5.5	1.5	3.5	0.5	3.0	0.5	3.0	4.0	13.5	1.5	3.0
$5^3.10^{-6}$	3.5	1.5	3.0	3.0	2.5	4.0	3.0	1.5	0.5	2.5	0.5	3.0	4.0	8.0	1.5	2.5
$5^4.10^{-7}$	3.0	3.0	3.5	4.5	3.5	3.0	2.0	3.0	1.0	2.5	1.0	2.5	6.0	6.0	2.0	2.5
$5^5.10^{-8}$	3.0	2.5	6.0	6.0	1.5	4.0	1.5	3.0	2.0	1.5	1.0	1.5	3.5	6.0	3.0	1.0

a Wasser mit Chininhydrochlorid
b Destilliert

II

Prüfung der Geschmacksempfindlichkeit auf Zitronensäurewasserlösungen der Waldrötelmaus (*Clethrionomys glareolus* Schreb.) des Degu (*Octodon degus* Mol.) und der Hausspitzmaus (*Crocidura russula* Herm.)

Bei den Versuchen bediente man sich mit 7 Exemplaren der Waldrötelmaus, mit 5 des Degu, und einem Herdchen von 5 Exemplaren der Hausspitzmaus.

Tabelle V

Clethrionomys glareolus Schreb.

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration der Zitronensäure in %	A		B		C		D		E		F		G	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
$5^2.10^{-5}$	12.0	22.5	4.5	9.0	5.0	4.0	1.5	2.5	1.5	3.0	1.5	3.0	13.5	9.5
5.10^{-4}	12.0	11.0	3.5	6.5	2.5	5.5	1.5	2.5	2.0	2.5	1.5	2.0	12.0	6.5
10^{-3}	14.0	8.0	4.0	7.0	3.5	5.0	1.5	2.5	2.0	3.0	1.5	3.0	9.5	7.0
2.10^{-3}	23.0	23.0	3.0	6.0	2.5	5.0	1.0	3.0	2.5	2.5	2.0	2.5	8.5	7.0
$2^2.10^{-3}$	24.0	17.5	3.0	5.5	7.0	2.5	1.5	2.5	3.5	3.0	1.5	3.0	7.5	9.0
$2^3.10^{-3}$	17.0	24.0	3.5	6.0	4.5	3.0	1.5	2.5	2.5	3.0	2.0	2.0	7.5	8.0
$2^4.10^{-3}$	26.0	15.0	5.0	5.5	5.0	4.0	0.5	3.0	2.0	4.0	1.5	2.5	9.5	9.5
$2^5.10^{-3}$	25.0	22.0	6.0	6.0	4.0	3.5	1.5	2.5	3.0	1.5	2.5	2.0	9.5	12.5
$2^6.10^{-3}$	18.0	8.5	11.0	4.0	4.0	4.0	1.5	2.0	2.5	2.0	1.0	3.0	6.0	7.0
$2^7.10^{-3}$	22.5	19.5	10.5	4.0	3.5	5.0	1.5	2.0	2.5	2.0	2.0	2.5	8.0	8.5
$2^8.10^{-3}$	6.0	16.5	7.0	1.0	2.0	5.5	1.5	1.0	1.5	3.0	1.0	2.5	2.5	8.5
5.10^{-1}	6.5	18.5	5.0	3.0	2.5	4.0	2.0	1.0	0.5	5.0	1.0	2.0	1.5	11.5
1.0	2.5	27.0	2.5	5.0	2.0	4.5	1.5	2.0	0.5	3.5	1.0	3.5	1.0	12.0
1.5	2.5	27.0	2.0	7.0	2.0	4.5	1.0	2.5	0.0	4.0	0.5	3.0	1.0	16.0
2.0			2.0	6.5	2.0	4.5	0.5	2.5	0.5	3.5	1.0	3.5	0.5	7.5

a Wasser mit Zitronensäure
b Destilliert

Zusammenstellung 3

Art	Testsubstanz	Durchschnittliche Wertmessung			Verlässigkeitsintervall	Verfasser
		der Geschmacksschwelle	der Abweisschwelle	Der Geschmackstoleranzgrenze		
Mensch	Weinsäure	0.015%				Tilgner und Baryłko-Pikielna 1959 a, b
Hausspitzmaus	Zitronensäure		0.0238%			
Kalb	Essigsäure			0.156 g/100 ml.		Bell 1959 a, b
Waldrötel maus	Zitronensäure			0.589%	0.156—1.022	
Degu	Zitronensäure			1.531%	0.729—2.233	
Ziege	Essigsäure			5.0 g/100 ml.		Bell 1959 a, b

Tabelle VI

Octodon degus Mol.

Tägliche Flüssigkeitsverzehrung in cm^3.

Konzentration der Zitronen säure in %	C		D		E		F		G	
	a	b	a	b	a	b	a	b	a	b
$5^2.10^{-5}$	2.5	8.0	9.0	1.0	7.0	13.0	3.5	2.0	2.0	3.0
5.10^{-4}	1.5	5.5	1.0	1.5	0.5	1.0	1.0	2.5	1.5	0.5
10^{-3}	2.0	4.0	1.0	1.0	2.0	0.5	1.5	1.0	1.5	1.5
2.10^{-3}	2.5	4.0	1.0	1.5	0.5	1.0	1.0	1.0	1.5	0.5
$2^2.10^{-3}$	4.5	5.0	3.0	0.5	1.5	1.5	2.5	3.0	0.5	0.5
$2^3.10^{-3}$	4.5	2.5	1.0	3.0	0.5	1.0	1.0	1.0	3.0	0.5
$2^4.10^{-3}$	8.5	0.5	3.0	0.5	8.0	10.0	5.5	2.5	1.0	1.0
$2^5.10^{-3}$	4.5	2.5	0.5	14.0	1.0	0.5	2.0	2.0	3.5	1.0
$2^6.10^{-3}$	6.5	6.0	2.0	0.5	3.0	13.5	3.0	1.5	4.5	0.5
$2^7.10^{-3}$	6.0	4.0	1.0	4.0	16.5	8.0	1.5	1.0	1.0	0.5
$2^8.10^{-3}$	6.0	3.5	1.5	1.0	5.0	4.0	1.0	3.5	0.5	1.0
5.10^{-1}	10.0	1.0	1.0	3.0	5.5	7.5	2.0	3.5	6.5	1.0
1.0	8.0	3.0	2.0	1.5	1.5	6.5	1.0	4.5	1.0	2.0
1.5	2.0	3.5	1.0	6.5	1.0	1.5	1.0	5.0	1.0	0.5
2.0	1.0	1.5	1.0	2.5	0.5	1.5	1.0	4.5	0.0	6.0
2.5	0.5	8.5	1.0	2.5	1.5	4.0	0.5	2.0	0.5	2.0

a Wasser mit Zitronensäure
b Destilliert

Tabelle VII

Crocidura russula Herm.

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration der Zitronen säure in %	A+B+C+D+E	
	Wasser	
	mit Zitronensäure	destilliert
$5^2.10^{-5}$	1.5	3.0
5.10^{-4}	2.5	2.5
10^{-3}	1.5	2.0
2.10^{-3}	2.5	1.5
$2^2.10^{-3}$	2.5	1.0
$2^3.10^{-3}$	1.5	2.0
$2^4.10^{-3}$	1.0	1.5
$2^5.10^{-3}$	0.5	1.5
$2^6.10^{-3}$	0.5	2.0
$2^7.10^{-3}$	0.5	2.5
$2^8.10^{-3}$	0.0	3.0
5.10^{-1}	0.0	2.5
1.0	0.0	2.5

Die Versuche begannen mit Verabreichung von sehr verdünnten Zitronensäurelösungen und einem stufenweisen Übergang zu immer stärkeren Konzentrationen. Die erste verabreichte Verdünnung war eine Säurelösung von 0.00025% und jede der nachfolgend verabreichten Lösungen hatte eine doppelt starke Konzentration als die vorhergehende, bis zum Augenblick in dem die Konzentration 0.25% betrug. Danach verabreichte man eine Lösung von 0.5%. Bei weiteren Versuchen wuchs die Konzentration der Zitronensäure gleichmässig um 0.5% an. Die Zitronensäurelösungen (und nachher die Sacharose- und Kochsalzlösungen) wechselte man in Tagesabständen ein, und um eine Desorientierung der Tiere zu vermeiden, wurden dieselben immer an derselben Seite des Käfigs verabweicht. Im Gegensatz zu den Hausspitzmäusen, deutet die Annahme von verhältnismässig hochprozentigen Konzentrationen der Säure durch die verbliebenen Tierarten darauf hin, dass die für dieselben erlangten Schwellen-Angaben die Geschmackstoleranzgrenzen darstellen. Durch Angaben anderer Verfasser ergänzte Forschungsergebnisse illustriert die Zusammenstellung 3.

III

Prüfung der Geschmacksempfindlichkeit auf Sacharosewasserlösung der Waldrötelmaus (*Clethrionomys glareolus* Schreb.) des Degu (*Octodon degus* Mol.) sowie der Hausspitzmann (*Crocidura russula* Herm.)

Bei den Versuchen bediente man sich mit 4 Exemplaren der Waldrötelmaus, 4 Exemplaren des Degu, sowie mit einem Herdchen (= 5 Stück) der Hausspitzmäuse. Die Versuche begannen mit Verabreichung von Vorschwellen der Sacharoselösungen, und einem allmählichem Übergang zu immer stärkeren Konzentrationen. Die erste Verdünnung, die verabreicht wurde, betrug 0.05%. Die nächst folgenden Konzentrationen waren um 0.05% stärker konzentriert als die vorhergehenden, bis zum Augenblick, in dem die Testlösung die Konzentration von 1% erlangte. Aus den Feststellungen, welche die Geschmacksschwelle der Menschen auf Sacharose betreffen und bezüglich der Auswahlschwelle bei Ratten (Richter und Campbell 1940a, b) sollten die Schwellenwertmessungen der von mir geprüften Tiere unterhalb der einprozentigen Lösung liegen. Die weitere Verabreichung von immer stärkeren Konzentrationen hatte als Ziel die Bestimmung der Grenze der Geschmackstoleranz. Jede nachfolgende Lösung, in Grenzen von 1—11% wuchs um 1% Konzentration an, und danach um 2% bis zu einer 19% Lösung. Von da ab wuchsen die folgenden Konzentrationen um 3% bis zu einer 34% Lösung und weiterhin um 6% bis zur gesättigten Lösung einschliesslich.

Man erzielte, beim Degu und bei der Waldrölmaus, Angaben die die Auswahlschwelle betrafen.

Die Hausspitzmäuse reagierten nicht auf die Schwellenwerte. Erst von einer ausdrücklich süssen (für den Menschen) Sacharoselösung ab, und zwar einer vierprozentigen Lösung, begann die Verzehrung der Testlösung durch dieselben anzuwachsen und erzielte bei einer 7% und der 9% Lösung ihre beiden Höhepunkte. Ihre Geschmackstoleranzgrenze bestimmt die 11—13% Sacharoselösung.

Tabelle VIII

Octodon degus M o l.

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration der Sacharose in %	A		D		F		G	
	a	b	a	b	a	b	a	b
0.05	0.5	2.0	2.0	1.0	1.0	1.5	3.0	0.5
0.1	2.0	1.0	5.0	2.0	1.5	5.0	2.5	1.5
0.15	4.0	0.5	0.5	2.0	0.5	0.5	1.5	0.5
0.2	2.0	2.0	4.0	1.0	1.0	2.5	1.0	1.0
0.25	2.5	1.0	1.5	2.5	1.5	1.5	2.0	1.0
0.3	1.0	1.5	10.5	1.0	3.0	1.0	1.0	2.5
0.35	3.0	1.5	8.5	1.5	6.5	1.5	6.0	2.0
0.4	5.0	1.0	8.5	1.5	7.5	0.5	11.0	1.0
0.45	5.0	1.5	15.5	2.0	8.5	1.0	6.5	1.0
0.5	8.0	1.5	19.0	1.0	6.5	1.0	4.5	1.0
0.55	9.0	0.5	20.0	1.0	11.5	1.0	6.0	0.5
0.6	7.5	1.0	10.0	1.0	8.5	1.0	6.0	1.0
0.65	7.5	0.5	8.0	1.0	6.0	1.0	5.0	1.0
0.7	9.0	0.5	6.0	0.5	4.5	0.5	5.0	1.0
0.75	7.0	1.0	8.0	0.5	5.0	0.5	5.0	1.0
0.8	7.0	0.5	5.0	1.0	4.0	0.5	4.5	0.5
0.85	5.0	0.0	6.0	0.5	3.5	0.5	4.5	0.0
0.9	6.0	1.5	6.0	0.5	3.0	1.0	4.0	1.0
0.95	8.0	0.5	5.0	0.5	4.0	0.5	4.0	0.5
1.0	11.0	0.5	22.0	0.0	4.0	0.5	3.5	0.5
2.0	10.0	1.0	15.0	1.0	12.0	0.0	3.5	0.5
3.0	13.5	1.0	34.0	0.5	9.5	0.0	3.0	0.5
4.0	16.0	1.0	—		5.5	0.5	5.0	0.0
5.0	15.0	0.5			15.0	0.5	9.0	0.5
6.0	13.0	1.0			20.5	1.5	13.5	0.5
7.0	14.5	1.0			30.0	1.0	17.0	0.5
8.0	17.0	0.0			32.0	0.5	13.5	1.0
9.0	30.0	1.0			37.0	0.0	13.0	0.0
10.0	31.0	1.0			38.5	0.5	11.0	0.0
11.0	34.0	0.5			39.0	0.0	11.5	0.0
13.0	36.0	0.0			36.5	0.5	20.0	1.0
15.0	33.0	0.0			35.0	0.5	25.5	1.0
17.0	26.5	0.0			18.5	0.0	20.5	0.5
19.0	19.0	0.5			25.0	0.0	15.0	0.5
22.0	18.0	0.5			16.5	0.5	17.0	0.0
25.0	11.0	0.5			14.5	1.0	18.5	0.5
28.0	12.0	0.0			15.5	0.5	13.5	0.0
31.0	10.0	1.0			12.5	0.5	11.5	0.5
34.0	10.0	0.0			18.0	0.0	11.5	0.0
40.0	9.0	1.0			11.0	1.0	9.5	1.0
46.0	11.0	1.0			13.5	0.0	11.0	1.0
52.0	8.5	0.5			9.0	0.0	9.0	1.0
58.0	7.0	1.0			10.0	0.0	10.0	1.0
64.0	5.0	1.5			11.0	1.0	8.0	1.0
67.0	5.0	1.5			5.0	1.0	7.0	1.0

a Wasser mit Sacharose
b Destilliert

Tabelle IX

Clethrionomys glareous Schreb.

Konzentration der sacharose in %	C		D		F		G	
	a	b	a	b	a	b	a	b
0.05	6.0	3.0	2.5	2.0	3.0	1.5	2.5	2.0
0.1	5.5	5.0	2.0	1.5	3.0	2.0	2.5	2.0
0.15	5.5	2.5	2.0	2.0	2.0	1.5	3.0	1.5
0.2	6.0	4.0	2.0	2.0	2.5	3.0	2.0	2.0
0.25	5.5	4.5	2.0	3.5	3.5	2.0	1.5	2.5
0.3	5.0	3.0	1.5	2.5	4.5	1.0	3.0	1.5
0.35	5.0	5.0	1.5	2.5	6.0	1.0	2.5	2.0
0.4	5.5	4.0	2.0	2.5	4.5	1.5	3.0	2.5
0.45	5.5	3.0	3.0	1.5	6.0	0.5	3.0	1.5
0.5	6.0	3.0	2.0	2.0	5.0	0.5	3.5	0.5
0.55	6.0	2.5	2.5	2.0	4.0	0.5	3.0	1.0
0.6	6.5	2.5	3.0	2.0	5.0	1.0	3.0	1.0
0.65	9.0	2.0	3.0	1.0	5.0	1.0	4.0	1.0
0.7	6.0	1.0	2.5	1.0	3.5	1.0	4.0	0.5
0.75	8.0	1.5	3.0	1.5	4.0	0.5	3.5	1.0
0.8	10.0	2.0	3.5	1.0	4.5	0.5	4.0	1.0
0.85	12.0	1.5	3.0	1.0	3.5	1.0	4.0	1.5
0.9	13.0	1.5	3.5	1.0	3.0	1.0	4.5	1.0
0.95	18.0	1.0	3.0	0.5	3.0	0.5	5.5	1.0
1.0	10.5	1.0	3.0	0.5	3.5	0.5	4.5	0.5
2.0	18.0	0.5	3.0	0.5	3.5	0.5	5.5	0.5
3.0	12.0	0.5	3.0	1.5	4.0	0.0	7.0	0.5
4.0	14.0	1.0	2.5	1.0	5.0	0.0	8.0	1.0
5.0	15.0	0.5	3.0	0.5	6.0	0.5	7.0	0.5
6.0	17.0	0.5	3.5	0.5	8.0	0.5	8.0	0.5
7.0	14.0	2.0	3.5	0.0	6.5	0.5	8.5	0.0
8.0	14.0	0.5	5.0	0.5	7.0	0.5	9.5	0.0
9.0	14.5	0.5	4.5	0.5	9.5	0.0	8.5	0.5
10.0	17.0	0.5	4.5	0.0	10.5	0.5	9.5	1.0
11.0	16.5	0.0	5.5	0.5	9.0	0.5	9.5	0.5
13.0	16.0	0.5	4.0	0.5	9.0	0.0	9.0	1.0
15.0	15.0	0.5	4.5	0.5	9.0	0.0	8.5	0.0
17.0	14.0	0.5	4.5	0.5	9.5	0.5	8.5	0.5
19.0	12.0	0.5	4.5	0.0	8.5	0.0	7.0	0.5
22.0	8.5	0.5	5.0	0.0	10.0	0.0	7.5	0.5
25.0	10.0	0.0	5.5	0.0	9.0	0.5	7.0	0.5
28.0	8.0	0.5	4.5	0.0	8.5	0.0	7.5	0.5
31.0	6.5	0.5	5.5	0.0	8.0	0.5	7.0	0.0
34.0	5.5	0.0	4.5	0.0	8.0	0.5	6.0	0.5
40.0	5.0	0.5	4.5	0.0	5.0	0.5	6.0	1.0
46.0	5.0	2.0	3.0	0.5	5.0	1.5	5.0	1.0
52.0	3.5	1.0	3.0	0.5	4.0	2.0	4.0	2.0
58.0	2.5	1.0	4.0	0.5	4.0	2.0	4.0	2.0
64.0	3.5	3.5	4.0	1.0	4.0	2.5	3.0	3.5
67.0	2.0	2.0	2.0	1.5	3.5	2.5	3.5	4.0

a Wasser mit Sacharose
b Destilliert

Tabelle X

Crocidura russula H e r m.

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration der Sacharose in %	A+B+C+D+E	
	Wasser	
	mit Sacharose	destilliert
0.05	2.5	4.0
0.1	3.5	3.5
0.15	3.0	3.5
0.2	2.5	3.5
0.25	3.0	3.5
0.3	2.0	3.0
0.35	2.5	2.5
0.4	2.5	2.5
0.45	2.5	3.5
0.5	2.5	3.0
0.55	2.5	2.5
0.6	2.0	3.0
0.65	2.5	2.5
0.7	2.5	2.5
0.8	2.5	3.0
0.85	3.0	2.5
0.9	2.5	2.5
0.95	3.5	2.5
1.0	2.5	2.5
2.0	2.0	2.5
3.0	2.5	2.0
4.0	3.5	4.0
5.0	5.0	3.0
6.0	6.0	3.5
7.0	8.0	3.0
8.0	9.5	4.0
9.0	7.0	5.0
10.0	9.5	5.0
11.0	9.0	6.5
13.0	7.5	7.5
15.0	2.5	6.5
17.0	3.5	7.5
19.0	0.5	6.5
22.0	1.0	6.5
25.0	1.0	8.0
28.0	0.5	8.0
31.0	0.5	9.0
34.0	—	—

Bei der Waldrötelmaus lag die Auswahlschwelle auf Sacharose in Grenzen von 0.25 bis 0.625; Das Verlässigkeitsintervall betrug 0.21 — 0.705% für die Art. Im Masse des Konzentrationsanwuchses der Sacharose vergrösserte sich ihre Verzehrung und erreichte verschiedene Maximalmengen bei den einzelnen Exemplaren. Bei einer weiteren Konzentrazionserhöhung des Zuckers reagierten die Tiere durch Verminderung der Verzehrung der Testlösung, deren Minimum auf eine der gesättigten Lösung sich nähernde Konzentration entfällt.

Diese letzte Erscheinung wurde durch eine grössere Wassernahme, ab Beginn von Verabreichung der 40% Zuckerlösung begleitet.

Zwei Exemplare tranken bis zur Sättigung der Sacharoselösung einschliesslich, grössere Mengen der Testlösung als des Wassers. Die zwei verbliebenen Tiere verzehrten bei einer 67% Sacharoselösung mehr Wasser als Testlösung. Dieses Divergenzresultat ermöglicht nicht die Grenze der Geschmackstoleranz auf Sacharosewasserlösungen für die Waldrötelmausart zu bestimmen.

Beim Degu schwankte die Auswahlschwelle für Sacharose in Grenzen von 0.268—0.335%. Das Verlässigkeitsintervall betrug 0.255—0.365%. Im Masse des Anwuchses der Konzentration der Sacharose erhöhte sich

Zusammenstellung 4

Art	Durchschnittliche Wertmessung für Sacharosewasserlösungen in %		Verlässigkeitsintervall	Verfasser
	der Geschmacksschwelle	der Auswahlschwelle		
Mensch	0.41			Richter und Campbell 1940 a
Ratte		0.5		Richter und Campbell 1940 a, b
Waldrötelmaus		0.458	0.21 —0.705	
Degu		0.309	0.255—0.365	
Katze	Keine Reaktion auf Schwellenwerte			Carpenter 1956
Hausspitzmaus	wie oben			
Maulwurf	wie oben			

anfänglich mit Beginn der Schwellenwerte ihre Verzehrung. Nachher konnte aber ein Absinken des Volumens der entnommenen Verdünnungen bei Lösungen derer Konzentration sich den 0.95% näherte, beobachtet werden. Bei einer weiteren Konzentration des Zuckers wuchs dessen Verzehrung heftig an, und erreichte ihre maximale Höhe bei einer 11—15% Lösung. Nachher konnte eine abermalige Abnahme des Volumens der entnommenen Testlösung notiert werden, immer jedoch, bis zur gesättigten Lösung einschliesslich, wurde die Testlösung viel williger als reines Wasser getrunken.

Nun folgt die Zusammenfassung der Angaben die das Verlässigkeitsintervall und die Auswahlschwelle der Sacharoselösung bei einigen Säugetierarten betreffen unter Berücksichtigung der Geschmacksschwelle des Menschen.

Da die Schwellenmittelgrössen für Sacharose sich bei der Waldrötelmaus und beim Degu nur gering unterscheiden, wurde die Wesentlichkeit dieses Unterschiedes mit Hilfe des t-Student-tests auf Prüfung der Wesentlichkeit der Unterschiede geprüft. Der erhaltene Testwert des t-Studentes beträgt: $t = 0.507$, dagegen der von den Tabellen der Testauslegung abgelesene Wert: $t_\alpha = 2.45$. Da aber $t < t_\alpha$ ergibt sich die Folgerung, dass der Unterschied unwesentlich ist und dass die Waldrötelmäuse als weniger empfindlich wie die Art *Octodon degus* auf die Schwellenwerte der Sacharosewasserlösungen nicht angesehen werden können.

IV

Prüfung der Geschmacksempfindlichkeit der Feldwaldmaus (*Apodemus sylvaticus* L.) des Degu (*Octodon degus* Mol.) und der Hausspitzmaus (*Crocidura russula* Herm.) auf Wasserlösungen von Kochsalz.

Bei den Versuchen bediente man sich mit 5 Exemplaren der Feldwaldmaus mit 2 Exemplaren des Degu sowie einem aus 5 Exemplaren bestehendem Herdchen der Hausspitzmaus. Man begann die Versuche mit Verabreichung von stark verdünnten Lösungen und einem späteren, stufenweisen Übergang zu immer stärkeren Konzentrationen. Die erste der verabreichten Lösungen des Natriumchlorids war eine 0.01% Lösung. Jede Konzentration nachfolgender Verdünnungen war um 0.01% stärker als die vorherige, bis zum Augenblick in welchem die Konzentration 0.1% betrug. Die darauf folgenden Konzentrationen wuchsen um 0.1% an bis zu 0.5% Lösungen. Zu allerletzt wurden 1.0, 1.5 und 2.0% Lösungen verabreicht.

Die Hausspitzmäuse reagierten auf die Schwellenwerte nicht und ihre Geschmackstoleranz stellte sich einer 1.845% Lösung NaCl gleich. Die Feldwaldmäuse reagierten ebenfalls auf die Schwellenwerte nicht. Ihre durchschnittliche Geschmackstoleranzgrenze betrug 1.36%. Rin

Zusammenstellung 5

Art	Durchschnittlicher Wert für Kochsalzwasserlösung			Verfasser
	der Geschmacks-schwelle	der Auswahl-schwelle	der Geschmackstole-ranzgrenze	
Ziege			4.689g/100 ml.	Bell 1959 a, b
Kalb			2.455g/100 ml.	Bell 1959 a, b
Degu		0.074%	ca. 2%	
Hausspitzmaus		keine Reaktion auf Schwellen-werte	1.845%	
Feld-Waldmaus			1.36%	
Maulwurf				
Mensch	0.065%			Richter und MacLean 1939
Ratte		0.0554%		Richter 1939

Apodemus sylvaticus L. **Tabelle XI**

Tägliche Flüssigkeitsverzehrung in cm^3

Konzentration des Kochsalzes in %	A		B		C		D		E	
	a	b	a	b	a	b	a	b	a	b
0.01	3.5	4.0	1.5	1.5	1.5	1.5	1.0	2.0	2.0	2.5
0.02	2.5	5.0	1.5	1.5	1.5	1.5	0.5	2.5	1.5	3.0
0.03	5.0	2.5	1.0	2.0	2.0	1.5	0.5	2.0	2.0	3.0
0.04	4.0	4.0	1.0	2.0	2.0	1.5	0.5	2.0	4.0	4.0
0.05	4.5	3.0	1.5	1.5	1.5	2.0	0.5	2.0	1.5	2.5
0.06	3.0	3.5	1.5	2.0	1.5	1.5	0.5	1.5	1.0	2.5
0.07	5.0	3.0	1.0	3.5	1.5	1.5	0.5	1.5	2.0	2.5
0.08	3.0	3.0	1.0	2.0	1.5	1.5	0.5	2.5	1.5	3.0
0.09	3.0	2.0	1.5	1.0	1.5	1.5	1.0	2.5	1.5	2.5
0.1	3.5	2.5	1.0	2.0	1.5	1.5	0.5	2.5	2.0	2.5
0.2	5.5	3.0	1.5	2.0	1.5	2.0	0.0	2.5	1.5	4.0
0.3	2.5	3.5	1.0	2.0	1.5	1.5	0.0	2.0	2.0	2.5
0.4	5.0	3.5	1.5	2.0	1.5	2.0	0.0	2.5	2.0	2.0
0.5	5.5	3.5	0.5	3.0	1.0	2.0		3.0	2.0	2.0
1.0	7.0	5.6	1.0	3.5	2.0	2.0		3.0	2.0	2.0
1.5	4.5	7.5	0.5	3.5	1.0	1.5		2.5	1.5	2.0
2.0	1.0	9.0	0.0	3.0	0.5	2.0		2.5	0.5	3.0

a Wasser mit Natriumchlorid
b Destilliert

Tabelle XII

Octodon degus L.

Tägliche Flüssigkeitsverzehrung in cm³

Konzentration des Kochsalzes in %	G		F	
	Mit Natrium-chlorid	destilliert	Mit Natrium-chlorid	destilliert
0.01	0.5	1.0	0.5	1.0
0.02	0.5	1.5	0.5	1.0
0.03	2.5	1.5	4.5	0.5
0.04	0.5	0.5	0.5	0.0
0.05	0.5	1.0	0.5	0.5
0.06	0.5	0.0	2.0	0.5
0.07	0.5	0.5	5.5	0.0
0.08	0.5	0.5	3.5	0.0
0.09	0.5	0.5	5.5	0.5
0.1	2.0	0.5	7.0	0.5
0.2	2.5	0.5	4.5	0.0
0.3	2.5	0.5	10.5	0.0
0.4	4.0	1.0	13.0	0.0
0.5	4.0	0.5	1.5	0.0
1.0	1.0	0.5	10.0	0.0
1.5	5.0	0.0	11.5	0.0
2.0	0.5	1.0	0.5	1.5
2.5	0.0	1.0	0.0	2.0

Tabelle XIII

Crocidura russula Herm.

Tägliche Flüssigkeitsverzehrung in cm³

Konzentration des Kochsalzes in %	A+B+C+D+E	
	Wasser	
	mit Natrium-chlorid	destilliert
0.01	1.5	2.0
0.02	1.5	2.0
0.03	1.5	3.0
0.04	2.0	1.5
0.05	3.0	2.0
0.06	2.0	2.0
0.07	2.0	2.5
0.08	1.5	2.5
0.09	2.0	2.0
0.1	2.0	2.0
0.2	2.5	2.0
0.3	2.5	2.0
0.4	1.0	3.0
0.5	2.0	3.0
1.0	2.0	2.5
1.5	2.5	4.0
2.0	2.0	4.5

Exemplar (D) wurde nicht in Rechnung genommen, denn es wies ständig eine besondere Neigung auf nur aus dem linken Trögchen (mit Wasser) zu trinken. Unter den Degu wies ein Exemplar eine sich der 0.94% Kochsalzlösung gleichende Auswahlgrenze auf, und der andere — eine der 0.54% sich gleichende. Die Divergenz der beiden Ergebnisse ist nicht gross, wenn man beachtet, dass Richter (1939) bei den Versuchen mit 12 Ratten Schwankungen der Auswahlschwelle auf NaCl in Grenzen von 0.35 bis 0.08% erhielt. Die Geschmackstoleranz des Degu entsprach einer fast zweiprozentigen Salzlösung.

Nachstehend, die Vergleichsangaben der Geschmacksschwelle, der Auswahlschwellen und der Geschmackstoleranzgrenze der Wasserlösungen von Kochsalz, beim Menschen und bei einigen Säugetierarten.

V

Die Geschmacksempfindlichkeit ist sogar im Rahmen einer Art manchmal verschieden und hängt von verschiedenen Ursachen ab. Die auf Menschen durchgeführten Versuche bewiesen, dass hier das Alter, das Geschlecht und die Erscheinung eines Geschmackskontrasten eine gewisse Bedeutung haben. Beim Menschen kann, zum Beispiel, nach einem salzigen Anreiz, das reine Wasser süsslich schmecken. Die Geschmacksempfindlichkeit auf saure Anreize wächst an nach einem süssen Anreiz (Tilgner 1957). Eine wesentliche Bedeutung hat der Sättigungsgrad des Organismus durch die Testsubstanz, insofern diese Substanz dem Organismus bedürflich ist. Dies wird, durch auf Ratten durchgeführte Versuche (Richter 1939), bezeugt. Während bei normalen Exemplaren die durchschnittliche Auswahlschwelle auf Natriumchlorid 0.055% betrug, reichte sie bei Ratten, deren Nebennieren entfernt wurden, bis zu 0.003%. Man sollte also bei Vergleichung von Ergebnissen verschiedener Verfasser höchste Vorsicht halten lassen.

Wie die 2. Zusammenstellung es veranschautlicht, sind die Maulwürfe (*Talpa europaea*) am empfindlichsten von allen geprüften Säugetierarten auf Chininhydrochlorid (also einer giftigen Substanz). Man könnte annehmen, dass dies mit der Reduzierung der Sehkraft des Maulwurfes in Verbindung steht, einem Faktor, der die optische Auslese des Futters erschwert. Was die Empfindlichkeit auf Chinin anbetrifft, befinden sich die Hausspitzmäuse an zweiter Stelle, und weiter kommen die Ratten, also die Tiere die lieber in der Dämmerung oder in dunkelen Unterkünften, Nahrung suchen. An weiterer Stelle befinden sich die Waldrötelmäuse. Dieselben benehmem sich am Tage an der Erdoberfläche aktiv. Die Optik spielt also bei ihrer Futterauwahl unzweifelhaft eine grössere Rolle als bei den vorher erwähnten Arten.

In der Zusammensetzung des Futters der Waldrötelmäuse sind scheinbar auch gewisse „bittere" Pflanzen eingegliedert. Die von mir gezüchteten Tiere dieser Art assen gern Blätter des Löwenzahnes und vielleicht kann ihre kleine Empfindlichkeit auf Chinin darauf zurückgeführt werden.

Die Degu-Exemplare wiesen eine kleinere Reaktion für den Chiningeschmack auf, als die Waldrötelmäuse. Dies ist wahrscheinlich darauf zurückzuführen, dass dieselben in natürlichen Bedingungen noch bitterere (für den Menschen) Pflanzen, als der Löwenzahn verzehren, und vielleicht auch darauf, dass durch den langen Aufenthalt in Gefangenschaft eine Abstumpfung der Emfindlichkeit auf Gifte enstanden ist (das Degu Exemplar stammte aus dem Frankfurter Tiergarten).

Aus der 3. Zusammenstellung ersieht man, dass die empfindlichsten der geprüften Säugetiere auf den Geschmack der Substanz, welche beim Menschen einen sauren Eindruck belässt, die Hausspitzmäuse sind. Dieselben nahren sich mit tiereschem Futter, das nicht sauer ist, und daraus kann wohl ihr Vorbehalt gegenüber der Zitronensäure abgeleitet werden. Eine beträchtliche Geschmackstoleranz anderer Arten der in der Zusammenstellung erwähnten Säugertiergattungen steht warscheinlich in Zusammenhang damit, dass sie die Pflanzenfressendetiere sind. Es ist bekannt, dass einzelne Pflanzen verschiedene Saüren, manchmal in grossen Mengen, enthalten.

Die 2, 3 und 5 Zusammenstellungen zeugen davon, dass die Verwandschaft unter einzelnen Tierarten in keiner greifbaren Verbindung mit dem Grad ihrer Geschmacksempfindlichkeit steht. Auf Chininempfindlichkeit weisen, zum Beispiel, die Waldrötelmaus und der Degu einen grossen Unterschied auf, obgleich alle beide zu den Nagetieren gehören (Rodentia) und gleichfalls Ziege und Rind, obgleich beide Wiederkäuer sind.

Eine änliche grosse Toleranzdifferenz der Essigsäure tritt im Rahmen der Hohlhörnigen, zwischen Ziege und Kalb auf. Auch in der Reaktion der Nagetiere auf Kochsaltz beobachtet man eine Divergenz zwischen der Ratte und dem Degu einerseits, und der Feldwaldmaus, obgleich die Ratten und Mäuse eine nähere Verwandschaft bindet, als die Ratten und die Degu.

Bei Zusammenfassung des oben Erwähnten erscheint es, dass Unterschiede der Geschamcksempfindlichkeit einzelner Säugetierarten hauptsächlich von der Zusammenstellung ihrer natürlichen Kost abhängig sind, worauf schon B e l l (1959a) seine Aufmerksamkeit lenkte, sowie von der Lebensweise bei Nacht, bei Tageslicht, ober- oder unterirdischen, und dem damit bei der Einschätzung der Nahrungsqualität verbundenem optischen Anteil.

VI

ZUSAMMENSTELLUNG DER ERGEBNISSE

1. Die durchschnittliche Abweisschwelle der Chininhydrochloridwasserlösungen stellte sich beim Mauwurf (*Talpa europaea* L.) 0.0000199 g/100 ml. gleich; bei der Hausspitzmaus (*Crocidura russula* Herm.) 0.00021 g/100 ml.; bei der Waldrötelmaus (*Clethrionomys glareous* Schreb.) 0.000368 g/100 ml.; beim Degu (*Octodon degus* Mol.) betrug die Abweisschwelle (Geschmackstoleranzgrenze?) der obengenannten Lösungen 0.0144 g/100 ml.

Das Verlässigkeitsintervall betrug beim Maulwurf 0.0000109—0.0000363 und bei der Waldrötelmaus 0.000101—0.000635 g/100 ml.

2. Die Abweisschwelle der Wasserlösungen von Zitronensäure betrug bei der Hausspitzmaus 0.0238% und die durchschnittliche Geschmackstoleranz betrug bei der Waldrötelmaus — 0.589%, beim Degu — 1.531%. Das Verlässigkeitsintervall betrug bei der Waldrötelmaus für die Geschmackstoleranzgrenze 0.156—1.022%, und beim Degu 0.729—2.233%.

3. Die durchschnittliche Auswahlschwelle für die Sacharosewasserlösung entsprach bei der Waldrötelmaus 0.458% der Testlösung, beim Degu — 0.309% der Lösung. Vertreter beider obengenannten Arten tranken gern Zuckerlösungen einschliesslich der gesättigten Lösung, und deswegen konnte die Grenze ihrer Geschmackstoleranz auf Sacharosewasserlösungen nicht bestimmt werden. Bei der Hausspitzmaus bestimmte diese Grenze die Testsubstanzlösung, mit einer zwischen 11 und 13% starken Konzentration. Der Zuverlässigkeitsinterwall betrug bei der Waldrötelmaus, in Bezug des Wertes der Auswahlschwelle 0.21—0.705 und beim Degu 0.255—0.365%.

4. Die durch den Verfasser vorgenommene Prüfung der Reaktion auf Natriumchloridwasserlösung einiger Säugetierarten ergab blos beim Degu eine Präferenz dieser Lösungen dem Wasser gegenüber. Seine Auswahlschwelle betrug 0.074% und die Geschmakstoleranzgrenze ca. 2%.

Die Grenze der Geschmackstoleranz auf NaCl—Wasserlösungen betrug bei der Hausspitzmaus 1.845% und bei der Feld-Waldmaus — 1.36%.

5. Die grösste Empfindlichkeit auf Chininhydrochlorid wiesen die Maulwürfe, also Tiere mit sehr schwacher Sehkraft auf, danach die Hausspitzmäuse, die am Tage in dunklen Gängen und erst bei Dämmerung an der Erdoberfläche Nahrung suchen. Eine kleinere Empfindlichkeit auf Chininhydrochlorid als die Maulwürfe und die Hausspitzmaus cha-

rakterisiert die Waldrötelmaus und den Degu, bei denen erstens die Sehkraft eine grosse Rolle bei der Nahrungsselektion spielen kann, und zweitens welche sich in der Natur oft mit für uns bitter erscheinendem Futter nähren. Von den geprüften Arten: Hausspitzmaus (*Crocidura russula*), Waldrötelmaus (*Clethrionomys glareolus*) und Degu (*Octodon degus*) zeigte sich am empfindlichsten auf Zitronensäure die Hausspitzmaus, also eine Art derer Ernärungsbasis tierische Nahrungmittel bilden.

Was die Empfindlichkeit auf Sacharose anbetrifft, erwiesen sich die hauptsächlich mit Pflanzenfutter nährenden Tiere —*Clethrionomys glareolus* und *Octodon degus*— empfindlicher als die Tiere —Maulwurf und Hausspitzmaus— die sich hauptsächlich mit tierschem Futter nähren.

Die Ergebnisse der mit Kochsalz durchgeführten Versuche berechtigen die Behauptung nicht, dass Arten, welche die tierische Nahrung bevorzugen, empfindlicher auf Natriumchlorid sind als Arten, welche die Pflanzennahrung bevorzugen. Sowohl der Maulwurf als auch die Hausspitzmaus und die Feld-Waldmaus reagierten auf Schwellenwerte der Natriumchloridwasserlösungen. Ausschliesslich beim Degu vermochte man die Auswahlschwelle dieser Substanz feststellen.

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GENESIS OF SOCIAL PARASITISM AMONG ANTS

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The origin of the so-called "slavery" in ants was first dealt with by Darwin in his work, *"On the Origin of Species"*. The raids of predatory ants to catch the pupae as a food constituted, in his opinion, a genesis of slavery. When the spoil is profuse, a part of uneaten pupae may hatch in the robbers' nest. Such incidentary hatching of pupae could be easier if they were naked as, for instance, in *F. fusca*. In fact, *F. fusca* is a slave ant most often met with. Thus, a colony in which accessory workers appear, without any additional expense of energy, gains an advantage over other colonies of the same species in their struggle for existence.

Darwin's hypothesis was rejected by Wasmann (1891, 1901—1902, 1905, 1906, 1908a, b, 1912) who maintained that incidentary hatching of pupae, snatched for foraging purposes, could not give rise to the instinct of slave-making. He supported his opinion by a fact that female ants do not take part in robbing raids and, therefore, the selection would be complex. Wasmann's views were backed up in 1952 by Raignier.

Viehmeyer (1910) criticized Wasmann's reasoning, affirming that originally female ants could participate in the raids and that some traces of such a behavior are recorded in *F. sanguinea* until now. Following the latter view and even extending it, Kutter (1958) considered this species female ants' participation in raids to be one of the manners of founding new nests. Females take part in robbing raids of *Harpagoxenus* (Viehmeyer, 1912, 1921) whose habits were regarded by Forel (1921—1923) as a transitory form between slave-making habits of *F. sanguinea* and of *P. rufescens*.

Apart from Viehmeyer's counterargument, in the opinion of the author the question of inheritance, undertaken by Wasmann in the

course of discussion, cannot settle the matter. The problem of inheriting characters (morphological, physiological, as well as behavioristic) by worker ants is open to discussion until the present. In the same manner, the existence of any separate caste characters in workers could be questioned precisely according to the principle that all their characters must come down to them from the females. The worker caste differs, however, in its own specific characters a certain part of which was undoubtedly acquired already after its separation as an individual case. Thus far, the problem of inheritance in social insects has not been definitely solved in the broadest sense and, therefore, cannot serve as an argument in the discussion of partial questions.

Emery (1909) tried to bypass genetic difficulties, putting forward a theory that, phylogenetically, the parasitic and slave-making species are derived from their hosts and slaves. This theory, accepted by Wasmann (1905), Escherich (1917), Kutter and Stumper (1950, 1951), Brown (1955) and others was formed on the principle that, in general, parasites and hosts, "slave makers" and slaves, are closely related to each other. This fact has been confirmed by systematic discoveries of Arnoldi (1933) and Kutter and Stumper (1950, 1951, 1952).

The author is not inclined to accept this theory since it is difficult to imagine a natural evolutionary process which could form a fully parasitic (and, therefore, harmful to the species) caste within a species. Even if such a caste would be developed (against the principle of natural selection), it could not be explained how did it come about that it left its native nest and separated as an individual species. It would be undoubtedly more useful, advantageous and much simpler (without the necessity of new forms of behavior) to remain in the nest since, as it is, this caste cannot exist independently and, afterwards, it must attack its formerly own nest, in the capacity of a strange species, in search for help-workers. If they were developed from the same species and never existed quite separately, it would be hard to explain how the considerable biological differences could arise and exist between them.

It seems, therefore, that there is no convincing proof in favor of Emery's hypothesis, while much speaks against it.

The author is of the opinion that this problem should be considered inversely: the parasitism does not depend on the relationship between species but that it rather requires a close relationship. Species, biologically and ethologically quite different, cannot coexist in a common nest. The coexistence in a common nest implies a common protection of progeny under adequate conditions for its development, strictly defined for each species; it also implies a common feeding, identical biocenotic and ecologic conditions and all these require that biological

demands of coexisting species should be similar and this occurs mostly in species, closely related to each other.

Forel found, for instance, that *F. sanguinea's* winter migration to new nests makes impossible any long coexistence of this species with *F. pratensis* in which there is no such habit although, in other respects, their ecology is very similar. Thus, a relatively small difference in the biology can be an obstacle in founding mixed colonies.

Similar is Viehmeyer's (1910) reasoning that a close relation allows to extend the instinct of the progeny protection to another species. Hölldobler (1948) and Gösswald (1952) estimated the biological relation of various species by a degree of easiness of mutual adaptation.

Thus, although the author does not exclude a possibility of the biological similarity that arose on another principle, different than the genetic affinity but it is most frequently that such similarity occurs between species genetically related and, therefore, in such species, the parasitic coexistence can be most easily reached. This can explain the fact that mixed colonies are most often met with in related species.

A question, why the species, coexisting in compound nests, may differ systematically and biologically, is answered by Wheeler (1904). He suggests that in such a case there is no common progeny rearing and, therefore, biological differences are a less important factor. According to the author, there are also no common feeding, no common building of the nest, etc.

A phenomenon of a temporary parasitism was discovered by Wheeler (1904, 1905, 1909) and proved to be significant for the problem of origin of slavery (Wasmann 1905, 1906, Piéron 1910). This phenomenon is caused by the fact that the females of many species of the genus Formica (*F. rufa, F. sanguinea, F. exsecta, F. truncicola*), as well as of other genera (in 1926, at least 17 species and 14 genera were mentioned by Wheeler) are unable to found independently a new nest. After a nuptial flight, such a female penetrates into the nest of a foreign species, for instance, of *F. fusca* (in the case of the genus Formica) and is adopted by its workers which subsequently rear the brood of this female.

The origin of this kind of behavior is ascribed by Wasmann to an original habit of solitary females, looking for the nests of their own species. This occurs in all species living in multi-nest colonies. This loss of the capability of an independent nest-founding was caused, according to Wasmann, by their manner of founding nests by branching. This was confirmed by Eidmann's (1929) statement that the *F. rufa* females

are deprived of the instinct of the brood protection which, however, was in turn denied by Hölldobler (1953).

Under artificial conditions, Kutter (1913) and Raignier (1938) achieved the adoption of the *F. sanguinea* females by the *F. fusca* workers. However, Gösswald (1951a, b, 1952) caused, also under artificial conditions, the adoption of various Formica by various species of the same genus. It is clear, therefore, that artificial experiments of this type do not prove the tendency to the adoption under natural conditions. On the other hand, it results from Gösswald's experiments that it is precisely *F. fusca* which is the least tolerant species, killing strange newcomers.

All this reasoning of Wasmann was contradicted by Emery (1909) who did not think that ants willingly accept the presence of strange females. He referred to Huber's (1810) opinion that the adoption of a female by her own species is a frequently recorded phenomenon which is quite enough to explain the manner of nest founding in the species discussed. A sudden passage from the adoption by own species to the adoption by a strange one is, in Emery's opinion (with which the author agrees), rather too great.

Brun (1913), Kutter (1913), Rüschkamp (1913) and Wasmann (1913) tried to evade these difficulties assuming that the adoption takes place in the nests of *F. fusca* in which there are no females of the latter species. Since, however, there cannot be a sufficient number of such nests and Wasmann (1915) himself observed only 4 such cases during a 18-year period of his investigations (the rarity of the *F. fusca* nests without females is explained by the polygeny of this species, recently discovered by Kutter, 1956), he assumes that a female of *F. fusca* may be killed by a strange female which penetrated into the nest of this species. He admits that thus far such a phenomenon was produced only experimentally and under artificial conditions, but, he adds, "*this occurs undoubtedly*" also under natural conditions.

Such a case is, however, excluded by Brun (1913) and, in the light of Gösswald's experiments, mentioned above, a possibility of the *F. fusca* workers letting a strange female into their nest and allowing her to kill their own one, seems highly improbable. However, a theory that this is a sole manner of the nest founding by *F. rufa* is subsequently supported even by Gösswald (1951, 1952) himself. The hypothesis about the temporary parasitism is, in the case of the Lasius, backed up by: Emery (1908), Wasmann (1910), Donisthorpe (1911), Crawley and Donisthorpe (1911—1912), Escherich (1917), Forel (1921—1923), Lomnicki (1922), Brun (1924), Stitz (1939), Gösswald (1938, 1939), Stumper (1950), Goetsch

(1953), Raignier (1952), Wilson (1955), Kannowski (1959) and others.

In addition to Emery's, Gösswald's and Brun's counter-arguments, denying the hypothesis about regular nest founding by an obligatory temporary parasitism (at least applied to the genus Formica), the author finds also an important althoug indirect proof, speaking against it, that is, if only one of the species mentioned, occurring usually in large numbers, founded its nests by this method only, then, many young mixed colonies should occur. Kutter (1918) expressed the opinion that such nests are relatively numerous but it was not confirmed by data of other authors. Thus, for instance, after some scores of years of field investigations, Forel mentioned only 3 mixed colonies. (1), *F. exsecta* — *F. fusca*, (2) *F. truncicola* — *F. fusca* and (3) *F. pratensis* — *F. fusca*. The author found only one nest of *F. exsecta* — *F. fusca* over a period of 12 years of field investigations. Wasmann, a main follower of this theory, also mentioned only a few similar nests. Thus, mixed nests are in the Formica (except for *F. sanguinea*) rather a fully exceptional phenomenon.

According to the author, the cases of mixed colonies occur in those species of Formica which rob strange nests of pupae and use them as a food. Pupae, which happen to remain uneaten, can hatch and may resemble in this way a temporary parasitism. It happens regularly in *F. sanguinea* since snatching of pupae is a permanent rule in this species, while in others, it happens only sporadically and, therefore, a mixed colony is a rarity. The occurrence of *F. fusca* in mixed colonies should be explained by a fact that robbing *F. fusca* of its pupae is very easy and that these pupae are naked.

Quite different is probably the case of the genus Lasius in which many mixed nests were found (Lannoy 1908, Emery 1908, Wasmann 1909, Crawley 1910, Donisthorpe 1911, Lomnicki 1922, Rüschkamp 1924, Verhagen 1930 and Pisarski, pers. comm.) As a matter of fact, these cases were questioned by Escherich who maintained that these might be compound colonies, sometimes difficult to distinguish in practice. On the other hand, a change in the behavior of *L. umbratus* which — in mixed colonies — abnormally got out to the surface, was recorded frequently (Lomnicki, Verhagen, Rüschkamp, Pisarski). This may speak in favor of a mixed nest and of a change in the mode of life, induced by another species.

The author believes that the problem of the occurrence of the temporary parasitism was presented by many authors in a rather exaggerated form. If occuring in some species, it certainly could not be ascribed to all of them, mentioned in literature, but it is only in few of them — that

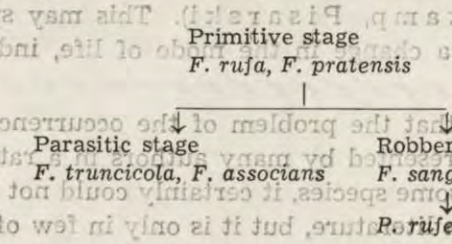
it could be determined as obligatory. Many species have been put on the list of temporary parasites only on the basis of a fact that their females were under artificial conditions, adopted by other species. Incidentally, a theory on the slavish mode of life of *F. truncicola* has been derived only on the basis of Wasmann's (1908a), artificial ant raising which does not seem by any means to be a sufficient proof. Similarly arranged experiments were carried out with similar results by Kutter (1956) who used for this purpose five other species. In other words, under artificial conditions the breeds of slaves can be raised independently of the biology of a given species.

Neither artificial slavery nor adoption of a strange female can be a sufficient proof for the existence of similar phenomena under natural conditions.

Tracing genetically the origin of the slavery from the temporary parasitism, Wasmann and Piéron base their reasoning on a fact that some species, practicing the temporary parasitism, remained in this stage, that is, after dying away of all workers of the host-species, they pass to the normal, non-parasitic mode of life, while other species (*F. sanguinea, F. truncicola,* etc.) currently supplement the number of workers by snatching pupae from other nests of the host-species.

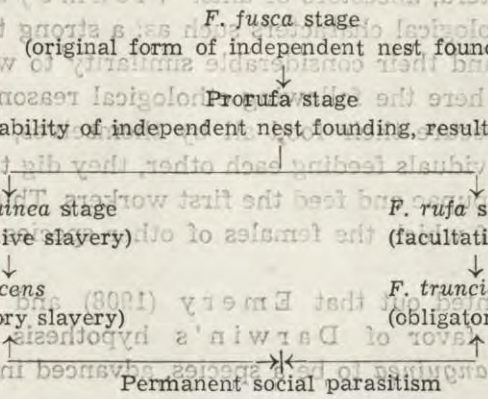
Such a view of the genesis of slavery was supported for the Myrmicinae by Santschi (1906), Arnoldi (1933), Bernard (1951), Raignier (1938, 1952), Brown (1955). Wheeler changed his mind several times. In 1901 he supported Darwin's hypothesis, whereas in 1905, he accepted Wasmann's theory, based on the occurrence of a temporary parasitism. In 1905-1906-1907, Wheeler revealed a separate character of nest-founding by *F. sanguinea:* the female of this species is not adopted in a strange nest (as *F. rufa* and others) but it penetrates into the nest as a robber, driving out or killing the workers and remaining in the nest only with pupae of which subsequently first slaves are hatched. This was confirmed for European forms by Viehmeyer (1908, 1909) and Wasmann (1908, 1910a, b).

Thus, the slave-making habit was derived by Wheeler, as well as by Wasmann, from the incapability of independent nest founding, based



on the fact that females cannot accumulate a sufficient amount of food. It can be shown in diagram as follows:

In the second edition of his monograph, Escherich (1917) extended and supplemented this diagram, giving in to a certain extent to Emery (1909), Viehmeyer (1910a) and Brun (1912) who held a belief that *F. sanguinea* cannot be derived from *F. rufa*:



In the above form, this diagram was accepted by Wasmann (1918) who mentioned that this is only a developmental series of certain biological conditions which cannot represent the phylogeny of particular species.

All this assumption can be criticized by means of Wasmann's own argumentation. Thus an instinct of capturing pupae could not be inherited by workers, practicing slavery, from their temporarily parasitic females since the temporary parasitism has nothing in common with raids in search for strange pupae. Such a female only lives in a strange nest, killing or not killing a previous female and driving out or not the strange workers. After hatching, its own worker-ants cannot find any strange pupae in the nest since the latter must hatch earlier. Thus, a question arises, where are stimuli which could cause a general departure of workers, leaving their nest and looking for strange pupae? According to the opinion of the author there are no evolutionary transitory forms and this statement is not a pure speculation but is based on observations and experimental studies which induce the author to question the views of the other authors and to deal once more with Darwin's hypothesis, although with a certain caution, i.e., the author maintains that *F. sanguinea* does not carry away pupae as slaves only, as Darwin believed, but that it is in an earlier evolutionary stage.

A theory of a primitive character of *F. sanguinea* was developed by Emery (1909), who was of the opinion that a parasite cannot evolve

into a robbing animal and that the only possible evolution is an opposite one. This view was backed up by Brun (1912) and, later on, by Wheeler (1926).

The serration of jaws in *F. sanguinea* is, according to Viehmeyer, a proof that this species is phylogenically older than *F. rufa*. He believed *F. sanguinea* to be a most primitive form and a direct descendant of the predatory Hymenoptera, ancestors of ants. Viehmeyer's arguments are based on morphological characters such as: a strong trunk, increased vitality of females and their considerable similarity to workers. Raignier (1938) added here the following ethological reasons: when founding nests, females secure their food all by themselves, they unite into groups of a few individuals feeding each other, they dig the soil, tear the cocoons of hatching pupae and feed the first workers. Thus, they perform several operations of which the females of other species of Formica are incapable.

It should be pointed out that Emery (1908) and Viehmeyer (1910a, b) were in favor of Darwin's hypothesis and, therefore, they considered *F. sanguinea* to be a species, advanced in a slavish mode of life.

The author backs up a view on the original, predatory descent of *F. sanguinea*. In addition to arguments, presented by Emery, Viehmeyer and Raignier, the author can quote the results of his own studies on the manner of foraging and carrying away pupae, practiced by this species.

As is well-known, a meat food is a predominant diet of *F. sanguinea*. Breeding of plant lice is, in this species rare and never practiced on any larger scale as it occurs in other species of Formica. The workers of *F. sanguinea* look for food individually as it was probably done by their predatory ancestors. Against the background of a social life, a tendency was developed in these ants to move in a direction already frequented by other individuals. This is the only species of Formica whose foraging grounds do not cover, more or less concentrically, the neighborhood of the nest. As a result of using paths, frequented by other workers, it happens in *F. sanguinea* that an area on one side of the nest is controlled by crowds of ants, sometimes, to a distance of several dozens of meters, while the other side remains almost not explored at all.

Twice over a few years, the author observed that a nest of *F. fusca*, situated 3 — 4 m from that of *F. sanguinea*, was never raided by its dangerous neighbors because precisely this area was not frequented by the workers of *F. sanguinea*. Such a phenomenon does never occur in *P. rufescens*.

Such manner of foraging causes a considerable concentration of work-

ers on a certain area. The ants are crowding only in places where a great amount of food has been found (for instance, at a strange nest with many pupae). This crowding does not occur as a result of mutual conveying information but only by an ever increasing concentration of individuals which are accidentally passing this place, as it occurs in all Formica (Dobrzańska 1958). Among others, this is proved by the facts, described above, that is, if a strange nest is not situated in a frequented foraging ground, it is never attacked by crowds of ants.

Now, it seems that the form of foraging of *F. sanguinea*, described above, is the third form of a social control of the terrain, next to the other two, previously described by Dobrzańska. It is no accident that Dobrzańska found a different behavior of *F. sanguinea* and did not assign it to any form of social foraging already established by her previously. Thus, to the two forms described by her, that is:

(1) social division of terrain (*F. rufa, F. pratensis* and *F. truncicola*),

(2) mutual conveying information on the spoil found (*Myrmica scabrinodis, Tetramorium caespitum, Leptothorax acervorum*),

the author would like to add the third form:

(3) expansive conquering of terrain, based on the tendency to use already frequented paths and directions *(F. sanguinea).*

The author believes that this disposition occurs in *F. sanguinea* in an initial, primitive form and so he shares the opinion of an early position of this species in the evolutionary development of social life. A further development of this character is manifested by an integrated army, operating as a team; this development takes place in the following two extreme directions, independent of each other:

(a) towards conquering and control of the terrain which develops against the background of the predatory mode of life and which, in its extreme form is expressed by repeated transferring of the entire nest along this path (Dorylinae); this way is followed by *Oecophylla* in which organized predatory raids often result in founding new nests (Ledoux 1949);

(b) towards slavery which develops from the general practice of carrying away the pupae (*P. rufescens*); *F. sanguinea* should be located in the very beginning of this way. Here, the question is of course not of phylogenetic bonds but only of possible development trends of certain properties of behavior.

This hypothesis of passing from the predatory state to the nomadic mode of life is incompatible with Malyshev's (1959) hypothesis of the separate derivation of Dorylinae from animals which did not found the permanent nests.

Thus, the author shares Emery's, Viehmeyer's, Brun's

and Raignier's view on the primitive character of *F. sanguinea* but with one reservation, that in his opinion, the behavior of this species is not a direct inheritance from its asocial, predatory ancestors which hunted individually. Moving in an already frequented direction, resulting in a mass foraging, is an element of behavior, developed already against the background of social life and is a proof of its advancement.

On the other hand, on the basis of his own works on *F. sanguinea* (Dobrzański 1961) and *P. rufescens* (Dobrzańska and Dobrzański 1960), backing up Darwin's hypothesis on the origin of slavery, the author is of the opinion that *F. sanguinea* is less advanced in this respect than it was believed by Darwin. The author thinks that this species is in a stage, envisaged by Darwin, in which carrying away pupae is a form of foraging and not yet a fully shaped instinct of slave-making. So, between the stage of *F. sanguinea* and the stage of *P. rufescens*, there would be the whole developmental cycle of forming the slave-making instincts, derived from the originally accidental hatching of strange pupae in the nest.

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BOOK REVIEW

Fiziologiia lobnykh dolei golovnogo mozga. Eksperimentalnoe issledovanie (Physiology of the frontal lobes. An experimental investigation). N. A. SHUSTIN. Edited by S. I. GALPERIN. Leningrad: Medgiz, 1959. Pages 221, illustrated.

In this monograph Naum Arkadevich Shustin, Sc. D., an experienced physiologist of the higher nervous activity at the Pavlov Institute of Physiology in Leningrad, presents his own findings based upon behavioral observations on dogs with prefrontal lobectomies located in front of the presylvian sulcus and large frontal lobectomies, involving prefrontal, premotor and parts of the motor cortex.

Shustin organizes his monograph around the effects of bilateral prefrontal and frontal lobectomies on the food salivary and motor conditioned reflexes (CRs), unconditioned reflexes (URs) and gross behavior. Emphasis is placed on the alterations in preoperatively acquired inhibitory CRs. The author shows that frontally lobectomized dogs are severely impaired on all three inhibitory tasks used, viz., trace conditioning, delayed conditioning and differentiation. Following large frontal lobectomies the previously two-phase course of the salivary outflow (scarce salivation in the first phase and abundant salivation in the second phase) during trace and delayed conditionings is totally lost: the salivary outflow is maintained at a relatively low level throughout the entire period preceding the reinforcement. In differentiation, the salivary CR to the presentation of the positive conditioned stimulus (CS) is greatly reduced and the inhibitory CR is left at the preoperative level, thereby giving an impression of an impairment or disinhibition of the inhibitory CR. After lobectomiess restricted to the prefrontal areas the salivary CR remains unchanged on positive trials and slightly increases on inhibitory trials, thereby showing a true disinhibition.

A few chapters cover methodology in a detailed and precise manner. Exact descriptions of the training of a variety of motor CRs in a free-choice situation are given. A unique feature is found in the sections dealing with the training of differentiation of objects with regard to their weight and form, training of a bar-pressing response or delayed responses, opening a door, walking in and out of a cage, etc. This part of the monograph is of particular interest since there is relatively little information in the behavioral literature on the establishment of complex habits in the dog. Evidence is presented that a large frontal lobectomy results in an abolition of the complex motor CR performance for a period of a few weeks to a few months, which is followed by the phase of an impairment of previously inhibitory CRs. The author relates the delayed response deficit in frontally lesioned animals to the impairment on trace CR performance, that is, on a task which is considered a form of internal inhibition in Pavlovian terminology. It is shown that

frontal dogs display a remarkable response perseveration in terms of an inability to shift from one response to another. A vocal (barking) CR is impaired parmanently after a large lobectomy and transiently after a prefrontal lesion. Control lesions of the temporal, parietal or occipital cortex do not abolish vocal CR performance. The unconditioned barking reaction is not affected after either frontal or any other cortical lesion. Simple habits, consisting of walking in and out of the cage, jumping over a barrier, etc. are not or slightly impaired postoperatively. They very often are perseverated.

The final chapters present findings on the susceptibility to the restraints of movement, ataxia of coordinated performance, perseveration of response, „following reflex", rotatory locomotion and disturbance in chewing and mastication associated with a protraction of the act of eating in frontally lobectomized dogs.

The author concludes that frontal lobectomy in the dog is associated with a regression to the unconditioned behavior patterns.

This monograph is a worthy contribution as the authoritative word of the original investigator. It may be recommended to anybody who deals with the cerebral cortex.

The principal deficiency of this monograph is its lack of describing the surgical procedure and the verification of brain lesions. The reader is unable to correlate the behavioral defects with frontal areas damaged. Another unsatisfactory feature is that the author bases his study and presentation on widespread damage to the frontal areas, subserving different functions.

Stefan Brutkowski, Warsaw, Poland

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