MAZE STUDIES WITH THE WHITE RAT

III. Anosmic Animals

HARVEY CARR
University of Chicago

Anosmic animals were employed to determine the function of olfaction in the environmental alterations described in the first paper. Records were secured from nine anosmic and five blind and anosmic rats. For these animals I am indebted to Miss Vincent. Professor Herrick made a histological examination of a group of seven of these defective rats. He reported that the operation was successful for two of the anosmic animals and for but one of the five blind and anosmics. From this record it is obvious that no conclusions drawn from the records of defective animals can be trusted without a subsequent histological examination. In our comparisons we shall utilize the data from the three animals of whose defective condition we are certain. Any conclusions from such a small group must necessarily be regarded with suspicion; however, we shall state the facts as they are and indicate their significance.

ANOSMIC ANIMALS

The anosmic operation exhibited no apparent deleterious effect upon the vitality of the animals. These animals were kept in the laboratory for nearly a year. Their appetite was undiminished; they looked sleek and well groomed, and the vigor and abundance of their activity was equal to that of normal animals.

One of the anosmic animals mastered the standard maze in two trials with a total error score of 40. The other rat required 21 trials and 127 errors to master the same maze. The average values for a group of 27 normal rats in mastering this maze were 18 trials and 144 errors. Evidently smell is not essential to the mastery of this type of maze. In this connection the construction of this maze must be considered; it was nearly water-tight and covered with closely fitting glass covers. Any

olfactory contact with the extraneous environment must have been greatly minimized.

In the cleanliness test a single error was made by one animal in the first trial. A pronounced disturbance was manifested by members of the normal and blind groups of animals. Presumably, the alterations in this experiment were primarily olfactory in character. The facts indicate that these novel disturbing conditions are sensed wholly or mainly by means of smell.

The maze was learned with one side of the top open. This top was now removed. No disturbance resulted; neither were normal animals affected.

Both animals were affected by the rotation of the heterogeneous environment. Their average error record was 2.50 and errors were present in 75% of the trials. The disturbing effect was practically eliminated when the test was repeated. The average error score per rat for the first test was 15. These results are similar to those obtained for normal animals.

Both animals were slightly disturbed when both maze and environment were rotated. The average error record was but .42 and the errors were confined to one-third of the trials. The adaptive capacity of this group was not tested. These results are similar to those for normal animals with the exception of a smaller error score. Taken at their face value, the facts indicate that anosmic animals are less sensitive to these changes than are normal or blind rats.

Rotation of the uncovered maze disturbed both animals. Their error record for the first test was 5.08, and the disturbance was present in 83% of the trials. A repetition of the test reduced the above values to 1.00 and 60% respectively. For the first test the normal records were 6.95 and 65%, while the corresponding values for the second test were 1.72 and 47%. These results indicate that anosmic animals are slightly less sensitive to these changes than are normal rats.

Variations in the position of the living cage exerted a pronounced disturbance with one rat and a slight disturbance with the other. The average error record was 5.00 and errors were present in 75% of the trials. These rats were subjected to a 24-hr. exposure before being tested. The results indicate a greater susceptibility than that of either blind or normal animals; a corrective function must be ascribed to olfaction in this case.

The cage was first rotated for the three new positions on successive days. No disturbance was manifested. Both blinds and normals were disturbed in similar conditions. This fact would indicate a sensitive function for olfaction. The rats were now left in each new position for five days and tested daily. No effect was observable for the first position. In the second position both rats manifested considerable hesitancy and indecision in nearly every run and one rat made eleven errors in one trial. The hesitancy and indecision were again apparent for the third position; one rat made fourteen errors in two trials, and the other eleven errors in one trial. Prolonged exposure thus induces a disturbance. The fact again indicates a defective sensitivity on the part of these rats.

These two anosmic rats belonged to a group of three animals, one of which died before the series of tests were completed. The record of this rat which was not histologically examined was similar in every respect to those given above.

A group of six anosmics were subjected to several tests on the sideless maze in the early part of the experimentation; these were not examined. Their results, however, were similar to those two which are known to be anosmic. The degree of disturbance was practically identical with that for normal rats in the following experiments,—position of experimenter, position of maze, and rotation of maze. They exhibited little evidence of any disturbance when the cage was rotated or altered in position.

BLIND AND ANOSMIC ANIMALS

Five such animals were tested and afterwards examined. All were pronounced blind. The anosmic operation was completely successful in but one case. Both olfactory bulbs were intact with one animal; evidently the bulbulous material in front of the olfactory lobes had been removed in this animal. With two animals the left lobe had been successfully removed while the right lobe remained intact or partly severed. In the remaining animal the sections were made through the frontal lobes of the cerebral hemisphere; on one side the section was sufficient to destroy olfaction; on the other olfactory connections were still possible. This group of rats thus consists of one blind, one blind and anosmic, two blind and partially anosmic,

and one which we may term a defective because of the loss of considerable cerebral tissue.

The learning records of this group of animals present many interesting features. The blind animal mastered the maze in 24 trials with a total error score of 152. After this time, the rat ran the maze consistently without error. This record is similar to those for blind and normal animals. Those two that were blind, and anosmic on the left side gave poorer records; one required 52 trials and 144 errors, and the second 102 trials and 508 errors. After the maze was mastered according to the criterion used, many errors kept appearing in an irregular manner for 25 to 40 trials. The blind and anosmic animal did still poorer; it required 130 trials and 2582 errors to learn this maze, but the act did not become thoroughly automatic until the 200th trial. It was also necessary to help this rat in 76 trials while learning the maze. In the early trials this animal utterly failed to reach the food box after several hours of effort and an error score of over 100. After the animal became exhausted I would stimulate it to further efforts and guide it when necessary. After the twentieth run I aided the rat whenever it became apparent that it was hopelessly lost. The defective rat required 194 trials and 1855 errors to master the maze. It was also helped in 32 of its trials. The act did not become thoroughly automatized for some time after the maze was considered learned. These results are significant because the difficulty of mastery is proportional to the degree of olfactory deficiency. The loss of either smell or vision does not operate as a detriment to the mastery of the maze; the loss of vision together with the partial or total destruction of smell is exceedingly detrimental. Evidently the deficiency due to the absence of either vision or smell is compensated in some manner by the other sense, while the remaining senses are unable to compensate for the deficiencies of both.

Rotation of the heterogeneous environment produced little disturbance upon the blind and anosmic or upon those which were blind and partially anosmic. The average error records for six trials were .33 and .66 respectively. The error record of the defective animal was 2.33. The normals gave a score of 1.90, the blinds 2.32, and the anosmics 2.50. Evidently the loss of both senses minimizes or practically abolishes the rat's sensitivity to these changes.

Uncovering the maze produced no effect. Neither was a disturbance manifested by the normals or the anosmics.

In the cleanliness test the blind and anosmic made 14 errors in one of its trials. Those which were blind and partially anosmic gave an error record of .50. These animals exhibited about the same degree of sensitivity as the anosmics. Their sensitivity was much less than that of either the normals or blinds.

Only one blind and partially anosmic animal was subjected to a rotation of maze and environment; its error record for six trials was 4.16, which is greater than those for normals or anosmics, but less than that for the blind rats.

The blind and anosmic was not affected by a rotation of the maze. A blind and partially anosmic rat gave an error score of 2.50, which is less than that for either anosmics, normals or blinds.

The blind and anosmic animal was not affected by changes in the position of the maze. The two which were blind and partially anosmic gave an error record of .75 which is less than that for any of the other sensory groups.

The blind and anosmic rat was disturbed by a rotation of the cage only after a considerable period of exposure to the novel situation. Errors were present in three of fourteen trials. The average error record was .78. The degree of sensitivity was about the same as that for the anosmics. The two blind and partially anosmic animals were more susceptible; their error record was 1.68 for eighteen trials. These animals were disturbed less than either the blind or normal groups.

A significant feature of these results is the practical insensitivity of the blind and anosmic rat to all alterations instituted after the mastery of the maze. A total of 50 trials was given, of which 80% were without error. The average error record for the 50 trials was 1.50. In the previous 50 runs, errors were absent in but 59% of the trials and the average error record was 2.70. This animal made a better record during the tests than during the later stages of increasing automaticity and after the maze was considered mastered. No errors were present in the first four experiments involving a total of 24 trials. The first indication of a disturbance was manifested in the fifth experiment in which the cage was rotated; a total of 11 errors was made in three of the 14 trials. The sixth test involved the

cleansing of the maze, and 14 errors occurred in the first trial. After the regular series of tests were completed, both cage and maze were rotated simultaneously in the hope of inducing more serious effects; error scores of 40, 5, and 1 were secured in three of the 10 trials. Rotation of cage and cleansing the maze were the only tests which induced disturbances, and it is possible that these results may have been due to chance irregularities. Granted the validity of the results, the question arises as to the sense avenue through which the changes were instituted. The changes resulting from cleansing the maze may well have been perceived through the sense of contact, for undoubtedly the contact values of the bottom of the runways were altered. Rotation of the cage may have affected the animal by means of its sensitivity to heat as the cage was located in the proximity of a steam radiator.

The practical insensitivity of the blind and anosmic animal considered in conjunction with the sensitivity of all other groups including those animals which were blind and partially anosmic indicates that all of these alterations are sensed almost wholly through smell and vision. This conclusion does not warrant the assumption that the rat does not possess any other efficient avenues of sensitivity. The statement merely means that smell and vision are the only senses adapted to the detection of these particular alterations of the environment.

Since vision and smell are the only effective senses in our conditions, it follows that all disturbances manifested by the anosmic group must have been instituted by means of vision, and that we can utilize the data of this group in determining the function of vision. This hypothesis is supported by the facts, for the results are in harmony with the conclusions as to the function of vision previously derived from the differential records of the blind and normal animals. All experiments involving an alteration of the optical environment were very effective upon the anosmic animals; this group of tests comprised rotation of environment, rotation of uncovered maze, and a change in the position of the living cage. On the other hand those experiments involving a minimal optical element, such as cleansing the maze and rotation of the covered maze, had little effect upon this group of rats. Moreover, the anosmic group when disturbed exhibited powers of adaptability on a par with

normal animals. This adaptive capacity was in evidence in the experiments in which the environment was rotated in reference to the maze, or the maze was rotated in relation to the environment. The records of these anosmic animals thus confirm our previous conclusion as to the sensitive and corrective values of vision.

The function of smell may be determined from several sources. 1. Since no other senses than smell and vision are concerned in these tests, the records of the blind rats must be due exclusively to the olfactory factor. 2. The differential sensitivity of the blinds as compared with those blind and partially anosmic must be interpreted in terms of smell. 3. The records of the normals as compared with those of the anosmic group must likewise be explained in terms of smell.

Smell possesses a sensitive function; by this statement we mean that these alterations do affect in some way the animal's behavior through the medium of olfaction. All three sets of facts support this conclusion. The blind and partially anosmic group suffered less disturbance than the blind rats in every experiment in which comparisons are possible. The anosmics on the whole manifested a lesser degree of sensitivity than did the normal animals; their sensitivity was much less for those experiments, e.g., cleanliness test, in which the olfactory element predominated. The blind animals, possessing only smell, exhibited the maximum amount of disturbance in those experiments in which the anosmic animals were the least sensitive. In the cleanliness test, those animals with smell intact,—blind and normal groups, suffered a pronounced disturbance, while but little effect was manifested by those groups in which olfaction was partly or completely eliminated.

In the previous paper, we noted that blind rats were sensitive to alterations of the environment, and concluded that these alterations operated as distractive stimuli rather than as motor controls. The results of this paper prove that smell is the main mediating sense involved in the detection of these changes by blind rats. No additional facts were developed necessitating a revision of the conclusion as to the distractive character of these olfactory stimuli.

Several significant features are contributed by the experiments concerning the functions of smell and vision in the mastery

of the maze. Anosmic animals learn the maze as readily as do normal rats. The olfactory operation produces no deleterious effect upon the vitality or behavior of the animals. The elimination of vision slightly decreases learning capacity, but this effect is limited to certain individuals; the vital capacity of certain rats is also lowered. The combined loss of smell and vision exerts some effect upon vitality, but this effect is apparently no greater than that resulting from the loss of vision alone. The combined loss of the two senses results in a pronounced decrease in learning capacity, an effect which can not be regarded as the arithmetical sum of the results of the two operations taken separately.

These facts indicate that the diminished vitality and learning capacity of the blind animals and the blind and anosmic groups can not be due to any effects of the operation *per se*, such as surgical shock, ether effects, etc. The anosmic operation is much more serious and difficult than the optic one, and any operative effects should be more evident and more extensive in the anosmic than in the blind groups. The reverse situation obtained; the anosmics were not affected while many of the blind rats were. The combined operation for the two senses is not any more prolonged or severe than for smell alone. If the operative effects are responsible for the deficiencies of learning capacity, one should expect as good records from the blind and anosmic groups as from the anosmic animals; as a matter of fact the anosmic animals suffered no deleterious effects while the learning capacity of the blind and anosmic rats was far below normal.

In the previous paper we noted three possible ways in which any sense might function in order to increase learning capacity. Sensitivity may be advantageous because of either a directive or tonic influence upon behavior and the vital activities. The removal of a sense organ may be disadvantageous not because of the elimination of sensitivity but because of certain deleterious effects of the operation itself. The directive function of vision for our conditions was decisively eliminated as one of the possibilities. The data of this paper also eliminates the third hypothesis. We are thus forced to conclude that the beneficial influence of vision upon learning capacity is due to the tonic and stimulative effect of retinal stimuli.

Similar possibilities obtain for the function of smell in the acquisition of the maze habit. The facts previously given exclude the hypothesis of operative effects for smell as well as for vision. As between the directive and tonic hypotheses no confident decision can be made. The records of the blind rats indicate that smell exerts no directive function after the maze is learned, but it is possible that olfactory controls may be utilized in the formation of the habit and yet be noneffective after the maze is mastered. The functions of smell and vision compensate for each other in the learning process. This fact is most easily interpreted on the basis that both senses have the same function. Since vision is efficacious because of its tonic effect, we would need to assume the same function for smell. On this hypothesis, a certain amount of sensory stimulation is necessary to induce sufficient motor activity requisite for learning. This effect can be secured through either smell or vision, while the elimination of both senses is disastrous. However, it is not entirely impossible to conceive that the two senses may compensate for each other even though their functions are different. One may suppose that vision exerts a tonic effect while the function of smell is that of control. There is good evidence that control is secured mainly through the medium of the cutaneous and kinaesthetic senses. One may now suppose that the cutaneous and kinaesthetic control requires a certain amount of supplementation and that this effect may be furnished by either the tonic function of vision or the additional control exerted by smell. A final fact supports the tonic hypothesis for both smell and vision. The blind and anosmic animals differed from the other groups in that they lacked persistence, initiative and incentive. I refer to the fact that these animals required help or additional stimulation in many of their trials. One possible interpretation of this fact is obvious; we may assume that these animals lacked a sufficient amount of sensory stimulation to arouse the motor activity adequate to the situation. Their activity was deficient in vigor, decisiveness, and persistence. These animals possessed the normal amount of energy, and the proper kind of stimuli for the control and direction of this energy, but they were so deficient in their sensory capacity that an adequate amount of this potential energy was

not released. Additional stimuli of an auditory or cutaneous character were requisite to overcome this deficiency.

The comparative data confirm our previous conclusion that the eye possesses some peculiar adaptive capacity. The adaptive power of anosmic animals is practically equal to that of the normals, while the capacity of both groups is much superior to that of the blind animals. The superiority of one group over another is thus not a matter of the number of senses, but rather of the kind of sense involved. Adaptation can not be conceived as a pure process of learning, since the blind and partially anosmic animals appeared to adapt as readily as did the blind rats although their learning capacity is much inferior. Neither can the differences in adaptive capacity of the various groups be due to operative effects, for on this hypothesis the adaptive ability of the anosmics should be inferior to that of the blind animals.

There is no conclusive evidence that smell is concerned in the process of adaptation. Although the blind rats did adapt to the distractive influences of olfactory alterations, it is entirely possible that this effect was mediated through the kinaesthetic-motor processes. There is some evidence that the distractions mediated through one sense can be corrected for through another. If smell is concerned in any overt manner in the process of adaptation, one would expect the adaptive power of normal animals to be greater than that of anosmic rats. Likewise blind rats should manifest greater ability than that possessed by blind and partially anosmic animals. There are no facts which indicate in any conclusive fashion the truth of either of these suppositions.

CONCLUSIONS

The results of this series of experiments confirm the conclusions of other investigators that the maze habit consists essentially of a tactual-kinaesthetic motor coordination.

This act is dependent, nevertheless, both during and subsequent to its development upon a wider sensory situation of which it is a part. This fact was proven by an experimental control of the relation between the animal and the environment.

The sensory connection between the act and those aspects of the environment which were altered was mediated almost exclusively through vision and smell.

The development of the act is contingent upon retinal impulses in two ways. On the one hand, retinal impulses operate as distractions, tending to prevent and delay the final perfection of the coordination. This distractive effect is present even when the relation of the visual environment to the rat remains stable. Any alteration of the environment from trial to trial increases the distractive effect. On the other hand, these retinal impulses tend to promote or condition the organization of the component elements of the act in so far as these impulses arouse the motor activity requisite to the solution of the problem. There are several ways of conceiving of this relation between visual stimuli and increased learning capacity. The experiment furnished no data for a choice between the several possibilities.

The development of the act is also dependent upon olfactory stimuli. No facts are pertinent as to the distractive or detrimental effect of these stimuli. Olfactory impulses, however, aid in the development of the act. These stimuli may be utilized as controls, or one may suppose that they are advantageous because of their tonic effect upon the various activities involved in the process of learning. No confident decision can be made as between these alternatives, though the latter hypothesis receives the greater support from the relevant data.

The act is still dependent upon these visual and olfactory stimuli after it has become thoroughly automatized, provided it was developed while these stimuli were present. The act can be acquired and function successfully when these stimuli have been completely eliminated. When the act was acquired while these stimuli were present, it will still function successfully when they are subtracted at least in part, or so long as their positional relations to the organism remain unaltered. Any positional change of these stimuli or the addition of new elements operate to disrupt or interfere temporarily with the successful functioning of the act. These changes of the stimuli function as distractions; they release impulses which the organism is unable to integrate successfully into the series of motor activities. The act is temporarily disrupted or disorganized.

Some degree of adaptation to these disturbances is the rule for all sensory groups. The experiments furnished no data which prove that smell is concerned in the process of adaptation. Vision certainly possesses an adaptive function. Of the

five suggested hypotheses as to the relation between vision and adaptation, two are disproven by the experimental data. Three possibilities remain. Adaptation may be a further process of automatization and rats with vision are at an advantage because of their greater learning capacity. Adaptation can not be explained wholly in terms of this conception as the adaptive capacity of the various groups of animals is not proportional to their relative learning ability. Visual adaptation may be a process of decreasing sensory susceptibility to the distractive stimuli. This conception can not wholly explain the phenomenon as certain facts indicate that vision can correct for disturbances mediated through other sensory avenues. Unaltered or familiar visual stimuli exert a quieting and reassuring effect upon the organism and enable it to resist the distractive effects of other stimuli. There are no facts which can not be explained fairly successfully on the basis of this hypothesis.

The maze act and the learning process are much more complicated phenomena than the conclusions of some previous investigators would indicate. The habit does not consist merely of tactual, kinaesthetic and motor elements. Other accessory and conditioning components are also present. Learning does not consist merely of the organization of certain tactual and kinaesthetic stimuli with certain movements. Many other sensory factors are present which release their quota of impulses that must be harmoniously integrated and organized in some fashion adapted to the solution of the problem.

All statements as to the functions of smell, vision, or other senses must be interpreted as applying only to the situations obtaining in these experiments.