SOME RELATIONS BETWEEN THE AUDITORY SYSTEM OF THE MEDULLA AND AUDITORY-STIMULUS FUNCTIONS¹

J. M. HARRISON, R. M. ABELSON, and G. L. FISHER

BOSTON UNIVERSITY

One approach to the relation between the nervous system and behavior is to consider the data of neuroanatomy as a series of independent variables, some of which may exert control over behavior. Such an approach requires the manipulation of the nervous system in a (neuroanatomically) known way in animals in which a large number of behavioral processes have been investigated. Since no one knows in advance what behavioral processes will be significant with respect to a given neural structure, the initial discovery of any empirical relations is largely a matter of luck. In this respect, one faces the same problems in the study of the effects exerted upon behavior by a particular drug.

It might be mentioned here that the foregoing approach is the opposite of that which seeks to determine the neural bases of a behavioral process, such as, for example, the neural basis of reinforcement.

The experiments reported here were carried out within this framework, and were concerned with the relation between some second- and third-order auditory pathways of the medulla and some functions of auditory stimuli. The effects of lesions of the auditory pathways on a variety of auditory- and visual-stimulus functions were examined in an effort to determine whether or not such lesions would differentially affect these stimulus functions.

In a second series of experiments the attempt was made at a preliminary analysis of the behavioral effects of the lesions by a method described by Dews (1956). In the present case the analysis consisted of the attempted reproduction of the behavioral effects of the lesions by the manipulation of the external environmental variables which control that behavior in the normal animal.

METHOD

Subjects and Behavioral Procedures

Eighteen male albino rats, Sprague-Dawley strain, were used in these experiments.

The animals were run on one or more of the following schedules.

(1) Noise termination (Keller). An intense noise (109 to 124 decibels) was continuously on unless terminated for 10 seconds by a lever press (R_p). Responses during the 10-second silent period were without effect.

(2) Termination-onset (Hefferline). This schedule was run with an intense noise (109 to 124 decibels) as the reinforcing stimulus. A depression of the lever (R_p) terminated the noise, and a release of the lever (R_R) produced the noise.

(3) Termination-onset. Same as the above schedule but with an intense light (200 foot lamberts) in place of the intense noise.

Details of the behavior generated by these schedules have been published elsewhere (Harrison & Abelson, 1959; Hefferline, 1950; Keller, 1941).

(4) Two-lever chain VI 1 CRF (limited hold). Responding on the first lever, L 1, produced either a low-intensity noise or a dim light, both of which were positive discriminative stimuli for responding on the second lever, L 2. A response on L 2 in the presence of the

¹The work reported here was supported by the National Science Foundation, Grant G.8678.

stimuli produced a 45-milligram food pellet. A limited hold of from 3 to 5 seconds was placed on the discriminative stimuli; and, in addition, responding on L 2 in the absence of the stimuli prolonged the VI interval on the first lever by 10 seconds. The sound and light stimuli alternated in an irregular manner on a variable-interval schedule of 2 minutes.

To allow the auditory-intensity threshold to be measured, this schedule was modified as follows. Each occurrence of the response in the presence of noise lowered the intensity of the next presentation of the noise by 2 decibels. Each occurrence of the noise that was missed was followed by an increase in intensity of 2 decibels of the next presentation. The threshold was defined as that intensity value of the stimulus that occurred most frequently.

Apparatus

For the aversive schedules the apparatus consisted of a light-tight and relatively sound-proof enclosure containing a restraining cage. Mounted in one wall of the restraining cage was a Gerbrands rat lever. Mounted over the cage was a tweeter loud-speaker for the delivery of the intense noise, while mounted at the side of the cage was a 32-watt, circular fluorescent lamp for producing the intense light. The contingent onset and termination of the noise were without noticeable transients, nor did the loud-speaker pick up any clicks from the operation of relays and other circuit devices. The starting characteristics of the fluorescent lamp were rendered suitable for use in aversive schedules by a circuit whose details were published elsewhere (Harrison & Warr, 1959).

The apparatus used on the VI 1 CRF schedules consisted of an enclosure and restraining cage similar to that described above. The two levers were mounted on adjacent walls of the cage, and the discriminative stimuli were delivered via a tweeter loud-speaker and a 5-watt bulb. Food pellets, 45 milligrams each, were delivered to a food cup from an Anger feeder. For the auditory-threshold measurements the stimuli of different levels of intensity were presented automatically. The number of times each intensity level was presented was recorded on counters.

The background noise in the enclosure, as measured by a Scott sound meter type 410 - C, varied between 60 and 70 decibels. The frequency spectrum of the background was unknown, and the extent to which this renders the absolute-threshold measurements really differential measurements could not be determined.

Behavioral Measures

The aversive schedules were run for 56-minute sessions. The mean response rates for R_p and R_R over the session for both schedules were calculated as follows:

$$\text{Mean rate } R_p = \frac{\text{Total number of } R_p \text{ in sound}}{\text{Total time sound on (min)}} \quad (\text{R's/min})$$

$$\text{Mean rate } R_R = \frac{\text{Total number of } R_R}{\text{Total time sound off (min)}} \quad (\text{R's/min})$$

Cumulative records were taken as follows. Each lever press, R_p , moved the pen stepper one division; the pen was displaced upwards ("reinforcement marker") during periods of silence. Thus, the return of the pen to the downward position indicates the occurrence of a release, R_R .

The discriminative schedule was run for sessions varying between 20 minutes and 2 hours. Cumulative records were taken of responding on the first (VI 1) lever. The number of presentations of each discriminative stimulus, the number of responses on L 2 in the presence of the discriminative stimuli, the number of responses on L 2 in the absence of the stimuli,

and the number of responses on the first lever were recorded on counters. For threshold measurement the stimulus values were presented automatically, and a record was taken on counters of the number of times each value was presented. Latency of responding to the discriminative stimuli was cumulated on a slow-speed clock, and individual latencies could be taken on a high-speed clock.

General Experimental Procedure

The general plan of the experiments was as follows. Animals were conditioned on either the termination or the termination-onset auditory schedules together with one or more of the other schedules to criteria of either stability or rate value. Since these experiments were carried out over a period of about 2 years, the actual criteria values varied so that the behavior for the last few sessions prior to operation is given below for each animal. Lesions were then placed in the ventral medulla with the intention of damaging the ventral second-order pathways while leaving the dorsal pathways intact. Following recovery from the operation, the schedules were again run, and they continued for a sufficient number of sessions to allow the effects of the lesion to be determined. This number varied between 5 and 38 daily sessions for the auditory schedules.

At the conclusion of the postoperative running, the animals were killed and the locus and magnitude of the lesions determined. The anatomical methods used together with the results will be published elsewhere (Harrison, 1960). For the purposes of the present paper the animals were divided into two classes: those with extensive (E) bilateral damage to either or both the large fiber pathway of the ventral acoustic stria and the lateral lemniscus, and those with minor (M) damage to these pathways. The experimental history of each animal is given in Table 1.

Table 1

Locus of Lesions and Behavioral Schedules of Experimental Animals

Animal	Lesion, L.L.	Lesion, V.A.S.	Sound aver.		Light aver.	Chain VI I CRF
<u>Schedule (Decibels)</u>						
B 13	M	M	T-O	111	T-O	—
BW 1	M	E	T-O	118	T-O	light and sound*
BW 4	M	M	T-O	118	T-O	light and sound
C 5	M	M	T-O	111	—	light and sound
C 11	E	M	T-O	124	T-O	light and sound
E 1	E	M	T-O	115	—	light and sound*
L 16	M	M	T-O	111	—	—
RA 4	M	M	T-O	124	T-O	—
RA 12	M	E	T-O	124	T-O	light and sound
Z 27	E	E	T	109	—	—
Z 32	M	E	T	109	—	sound
Z 39	M	E	T	116	—	—

Lesion, L.L., lesion of lateral lemniscus; Lesion, V.A.S., lesion of the ventral acoustic system; Sound aver., sound-aversive schedule; Light aver., light-aversive schedule; M, minor lesion; E, extensive lesion; T-O, termination-onset schedule; T, termination schedule.

Sound intensities measured on Scott meter, type 410 - C.

*Intensity threshold (sound) measured.

At the conclusion of the above experiments the attempt was made to duplicate some of the effects of the lesions by the manipulation of the parameters of the schedules. The details of the manipulations are given below for each animal.

RESULTS

Aversive Schedules, Rp

Figure 1 shows the average rate of Rp for the last three preoperative and all the postoperative sessions for all animals. The animals were classified into those having extensive (E)

Figure 1. Average rates of press for the last three preoperative and all postoperative sessions for all animals. E indicates extensive and M minor lesions. Solid line, sound; dashed line, light; vertical line, operation. Rates greater than 10 per minute were plotted at 10 per minute.

and those having minor (M) lesions of the auditory system. An inspection of the figure shows that extensive lesions reduce the average rate of the Rp on the auditory schedules to a value consistently below the preoperative values, while having little effect upon the rate of Rp on the visual aversive schedules.

Examples of the changes in the cumulative records of the auditory schedules produced by extensive lesions are shown in Fig. 2 and 3. In the case of BW 1 (Fig. 2), behavior on the schedule rapidly declined during the first 4 postoperative days to a very low level of a few responses per session. This decline occurred in 80% of the animals, and is the typical course of behavior following large lesions of the ventral acoustic system. Since from 7 to 19 days intervened between the last preoperative and the first postoperative sessions, this decline may be an example of a weakened "lay-off" effect as described elsewhere (Harrison & Abelson, 1959). The cumulative records of Z 39 (Fig. 3) show the highest level of responding found in the present series of animals with extensive lesions. The postoperative rate of Rp in this animal (which had a very extensive lesion) was about one-tenth of the preoperative rate. Since the postoperative rate of responding of Z 39 is about 10 times the operant level, the responding must be considered as residual behavior generated by the schedule. From consideration of BW 1 and Z 39, the effect of the lesion on Rp appears to be a reduction in rate, but not necessarily to zero.

The effect of a minor lesion upon the cumulative record of responding on the auditory schedule is shown in Fig. 4 (Animal BW 4). A transient change occurred in the record following operation, but within 7 days (sessions) it approximated its preoperative appearance.

Figure 2. Animal BW 1. Noise termination-onset schedule. Cumulative records: A, 36th hour (last hour prior to operation); B, C, D, E, F—1st, 13th, 24th, 26th, 32nd postoperative hours. Upward displacement, sound off on this and subsequent cumulative records of T-O schedule.

Figure 3. Animal Z 39. Noise-termination schedule. Silent period, 10 seconds. Cumulative records: A, 1st hour (5th hour prior to operation); B, C, D, E, F—1st, 20th, 22nd, 30th, 37th postoperative hours. In this figure, reinforcement mark indicates sound termination.

Aversive Schedules, R_R

The average rate of R_R over each session is shown for the last three preoperative and all postoperative sessions for all animals in Fig. 5. An inspection of this figure reveals that extensive lesions of the auditory system raise the rate of releasing on the auditory schedule while having little effect upon the release rate on the visual aversive schedule. Minor lesions of the auditory system were without effect upon the rate of release on both auditory and visual aversive schedules. In all the affected animals the release rate on the auditory schedule tended to approach its high value over the first three or four postoperative sessions in a manner analogous to the postoperative decline in rate of R_p .

The effect of an extensive lesion of the auditory system on releasing is shown in Fig. 2. Following operation, periods of no sound (pen displaced upward) become progressively shorter over the first few days until, ultimately, a press is followed by a release within an average of 3 seconds. (See *a* of Fig. 2.) The lack of effect of a minor auditory lesion on releasing is shown in Fig. 4.

Chain VI 1 CRF

Responding on L 2 (momentary discrimination with a limited hold) for all animals is given in Table 2. The behavior was expressed by taking the ratio of the average percentage of possible reinforcements received postoperatively to average percentage preoperatively.

Two animals (C 11 and RA 12) showed a postoperative loss of control of responding on L 2 by the sound. Light continued to control responding in C 11, so it appeared that the auditory loss was due to factors specific to auditory stimulation. The attempt was made to recondition C 11 using a high-intensity noise (111 decibels) as the discriminative stimulus, but no stimulus control was obtained. In the case of RA 12, it will be noted that the light stimulus disturbed the control of responding considerably. This suggests that the auditory loss may not be due, solely, to auditory factors.

Table 2

Ratios of Postoperative to Preoperative Response Strengths for all Schedules as a Function of Extensive and Minor Lesions of Acoustic System

Animal	Lesion	Sound aversive		Light aversive		Chain VI 1 CRF	
		R _p	R _R	R _p	R _R	%PR, light	%PR, sound
C 11	E	0.017	9.72	1.92	1.97	0.87	0.01
BW 1	E	0.027	14.43	3.70	0.26	0.95	1.04
RA 12	E	0.044	11.63	1.46	0.63	0.62	0.01
E 1	E	0.045	15.67	—	—	1.04	0.96
Z 27	E	0.057	—	—	—	—	—
Z 39	E	0.1	—	—	—	—	—
Z 32	E	0.127	—	—	—	—	1.05
C 5	M	0.95	1.31	—	—	1.00	1.03
RA 4	M	1.23	1.10	1.10	1.30	—	—
BW 4	M	2.00	0.96	0.72	1.00	1.03	0.98
L 16	M	2.125	2.26	—	—	—	—
B 13	M	4.08	3.07	—	—	—	—

R_p, ratio of the average rate of lever pressing (all sessions) postoperatively to average rate of lever pressing preoperatively; R_R, ratio of average rate of lever releasing (all sessions) postoperatively to average rate of lever releasing preoperatively; %PR, ratio of percentage of possible reinforcements obtained postoperatively to percentage obtained preoperatively; E, extensive damage of either the large fiber pathways of the ventral acoustic system and/or the lateral lemniscus; M, minor damage.

Table 2 indicates that Animals BW 1, E 1, and Z 32 showed no discriminative loss in spite of extensive auditory lesions and loss of responding on the auditory aversive schedules. Animal BW 1 showed a postoperative increase of threshold on the discriminative schedule of 10 decibels. Animal E 1 showed an increase in threshold of 20 decibels. No animal with minor lesions showed loss of light or sound discriminations.

Figure 6 shows the percentage of possible reinforcements obtained per session and the rate of responding on L 2 in S^A for BW 1. Clearly, the lesion had no effect on the stimulus control of responding on L 2. This result may be compared with the change in behavior of this animal shown in Fig. 1 and 2. Also shown in Fig. 6 is similar behavior for Animal C 11. The loss of control of responding on L 2 by the auditory stimulus was virtually complete. Light control was unaffected.

Figure 4. Animal BW 4. Noise termination-onset schedule. Cumulative records of the 33rd, 34th, 35th hours (last hour prior to operation) and the 1st, 4th, 7th postoperative hours.

A summary of the behavior of all the animals on all the schedules is given in Table 2. The horizontal line divides the animals into a group with extensive lesions (above the line) and a group with minor lesions. Inspection of the table reveals the following points.

The ratios of postoperative to preoperative rates of R_p and R_R on the auditory aversive schedules in animals above the line differ by a large factor from the ratios of the same rates of animals below the line. The ratio of rates of R_p and R_R on the light-aversive schedule are essentially the same above and below the line and also do not differ materially from the sound-aversive ratios below the line. Taking these observations together, it appeared that extensive lesions of the ventral acoustic system differentially affected responding on the sound- and light-aversive schedules.

Both small (0.01) and near-unitary values of ratios of percentage of possible reinforcements (sound) occur in animals with extensive auditory lesions. These data taken together with the data mentioned in the above paragraph indicated that extensive lesions of the acoustic system *differentially affected the control of behavior by auditory stimuli*.

ANALYSIS

The nature of the changes in auditory-stimulus control produced by the lesions of the auditory system may be investigated by the attempted reproduction of these changes in normal animals through manipulation of the variables which have been shown to control the affected behavior. Two experiments were carried out within this framework and are reported below.

Removal of the Intense Noise

Inspection of Fig. 1 suggested that behavioral changes produced by lesions may be similar to those produced by the removal of the noise in the termination-onset schedule. To determine the effects of this operation on the behavior generated by the schedule, four animals were conditioned under the standard conditions. The animals were then laid off for from 1 to 4 days. Daily running for at least 14 days was then recommenced under identical conditions except that the amplifier which supplied the noise was not turned on. Hefferline (1950) refers to this procedure as up-response restoration.

A summary of the changes produced in the average daily rates of R_p and R_R by the removal of the noise is shown in Fig. 7 for all animals. Cumulative records from two of these animals, BW 38 and BW 36, are shown in Fig. 8 and 9.

Changes in R_p . Removal of the noise produced an immediate reduction in the rate of R_p in all animals. Animal BW 37 showed a further decline from the rate on the first no-noise

Figure 5. Average rates of release for the last three preoperative and all postoperative sessions for animals on termination-onset schedule. E indicates extensive and M minor lesions. Solid line, sound; dashed line, light; vertical line, operation. There are no plots for sessions during which no presses occurred.

Figure 6. Percentage of possible reinforcement and rate of responding on Lever 2 in S^A for Animals BW 1 and C 11.

Figure 7. Effects of noise removal upon average press and release rates on Animals BW 36, BW 37, BW 38, BW 41. Vertical line indicates removal of noise.

day, but the other animals showed no consistent trend. These changes in the rate of R_p are essentially the same as those produced by the auditory lesions. This suggests the possibility that the effect of the lesion on R_p may be equivalent to turning off the noise.

Changes in R_R . Inspection of Fig. 7, 8, and 9 indicates that the animals fall into two groups with respect to changes in average rate of R_R produced by removal of the noise. In two animals, BW 37 and BW 38, removal of the noise had little effect upon the release rate for 8 to 9 days. In the other two animals, BW 36 and BW 41, removal of the noise immedi-

Figure 8. Animal BW 38. Noise termination-onset schedule. Cumulative records: A, 16th hour on schedule; amplifier off during B, C, D, E, F—1st, 5th, 6th, 7th, 13th hours after change of condition.

ately increased the rate of releasing to the operant level. The auditory lesions produced an immediate increase in rate of R_R in all animals. In the absence of further data the effect of the lesions on the rate of releasing cannot be concluded as equivalent to turning off the noise.

Reduction in Intensity of the Noise

The differential effect of auditory lesions upon aversive and discriminative functions of auditory stimuli together with the increase in discriminative threshold suggested the possibility that the lesions raise the threshold of all auditory-stimulus functions. On this assumption the intensity of the noise (109 to 124 decibels) would be below the aversive threshold postoperatively. An investigation of the aversive-threshold region published elsewhere (Barry & Harrison, 1957) gave results with respect to R_p that differ from the behavioral

Figure 9. Animal BW 36. Noise termination-onset schedule. Cumulative records: A, 18th hour on schedule; amplifier off during B, C, D, E, F—1st, 4th, 5th, 6th, 7th hours after change of condition.

changes produced by the lesion. However, in this study, cats were used rather than rats, and only the termination schedule was investigated. To obtain a more comparable picture, two animals (GF 10 and GF 11) were conditioned on the termination-onset schedule at 118 decibels, given a 3-day lay off, and run for an additional 14 days at an intensity of 97 decibels (a reduction in intensity of 21 decibels).

Changes in the mean daily rate of pressing and releasing produced by lowering the intensity are shown in Fig. 10 for both animals. Sample cumulative records from one of these animals (GF 11) are shown in Fig. 11.

As can be seen from Fig. 10 and 11 the behavioral changes produced by lowering the intensity of the noise by 21 decibels were quite different from the effect of the lesion. (See Fig. 2.) Thus, the effect of the lesion is not simply one of shifting the threshold of all auditory-stimulus functions by about 21 decibels.

SUMMARY

The purpose of the present experiments was to investigate the effects of lesions of the ventral acoustic system of the medulla upon auditory-stimulus functions. Rats were run on one or more of the following schedules, received lesions of the auditory system, and were re-run for a sufficient number of daily sessions to determine the behavioral effect of the lesions. The schedules on which the animals were run were as follows.

Aversive. Termination-onset. Intense noise as the noxious stimulus. Termination. Intense noise as the noxious stimulus. Termination-onset. Intense light as the noxious stimulus.

Figure 10. Rates of pressing and releasing produced by lowering intensity for Animals GF 10 and GF 11. Solid line, press; dashed line, release.

Figure 11. Animal GF 11. Noise termination-onset schedule. Cumulative records: A, 14th day high-intensity schedule; B, C, D, E—1st, 8th, 11th, 12th hours at reduced intensity.

Discriminative. Chain VI 1 CRF (limited hold). Noise as the S^D. Chain VI 1 CRF (limited hold). Light as the S^D.

The results were as follows.

Extensive lesions of the ventral acoustic system or the lateral lemniscus reduced the rate of pressing and raised the rate of releasing on the auditory aversive schedules. The lesions had no effect upon responding on the visual aversive schedule.

Extensive lesions of the ventral acoustic system had no effect on responding on the VI 1 CRF chain (with either light or sound as S^D) in three of the five animals in which responding on the auditory aversive schedules was affected.

Two analytical experiments were carried out as follows.

Four animals were conditioned to the standard criteria on the auditory termination-onset schedule. The noise was then turned off and remained off for the next 14 sessions. The effect of this was to reduce the rate of pressing (Rp) by about the same amount as lesions of the auditory system. The rate of releasing was increased in two animals and not affected in the other two. It was concluded that the effect of auditory lesions on the release rate was not equivalent to turning off the noise.

Two animals were conditioned to the standard criteria on the auditory termination-onset schedule. The intensity of the noise was then reduced by 21 decibels for the next 14 sessions. The changes in the rates of pressing and releasing produced by this intensity change did not resemble changes in these rates produced by the lesions of the auditory system.

REFERENCES

- Barry, J. J., Jr., and Harrison, J. M. Relation between stimulus intensity and strength of escape responding. *Psychol. Rep.*, 1957, **3**, 3-8.
- Dews, P. B. Modification by drugs of performance on simple schedules of positive reinforcement. *Ann. N. Y. Acad. Sci.*, 1956, **65**, 268-281.
- Harrison, J. M. Some behavioral functions of the lower auditory pathways in the rat. *J. Comp. Neur.*, in press.
- Harrison, J. M., and Abelson, R. M. The maintenance of behavior by the termination and onset of intense noise. *J. exp. anal. Behav.*, 1959, **2**, 23-42.
- Harrison, J. M., and Warr, B. An instant-start circuit for fluorescent lamps. *J. exp. anal. Behav.*, 1959, **2**, 226.
- Hefferline, R. F. An experimental study of avoidance. *Genet. Psychol. Monogr.*, 1950, **42**, 213-334.
- Keller, F. S. Light aversion in the white rat. *Psychol. Rec.*, 1941, **4**, 235-250.

Received February 19, 1960.