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Suppression of 60-Hz induced convulsive behavior by 3-Hz brain stimulation

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These experiments investigated the effect of 3-Hz brain stimulation on behavior induced by 60-Hz stimulation.

The "kindling effect" has been investigated in a number of laboratories (e.g., Gaito, 1976c; Goddard, McIntyre, & Leech, 1969). This effect involves a change from normal exploration (Stage 1, NE), to behavioral automatisms (Stage 2, BA—chewing, eye closure on ipsilateral side, salivation), and finally, to clonic convulsions (Stage 3, CC) in response to electrical stimulation of a specific brain site (e.g., amygdala). Stage 3 behavior involves the rat standing on its hind paws and bilateral convulsions of the forelimbs occurring. Behavioral, chemical, electrophysiological, and neurological aspects of this effect have been investigated by many researchers (Gaito, 1976b).

Gaito (1979) found that stimulation with 3-Hz sine-wave current following the induction of convulsive behavior via 60-Hz stimulation produced a suppression of convulsions in many rats. In the present paper, experiments are reported in which the concern was with (1) a further evaluation of the effect of 3-Hz brain stimulation upon rats that had achieved the convulsive stage, and (2) the effect of 3-Hz stimulation upon the development of the convulsive state.

EXPERIMENT 1

Method

Twenty male Wistar rats (about 130 days of age) were implanted unilaterally with bipolar electrodes in the amygdala. The brain coordinates for electrode implantation were the same as in previous experiments: .5 mm posterior to bregma, 4.5 mm from midline, 8.5 mm from skull (Gaito, 1976c).

Stimulation trials began 1 week after electrode implantation. For one group of eight rats, the first trial each day consisted of a 60-Hz sine-wave current for 30 sec into the amygdala using a Lafayette sine-wave stimulator. Two other trials with 3-Hz stimulation were provided approximately 1 h apart. This was the 60-3-3 group (Table 1). Stimulation was at an intensity of 100 microA for 20 trials. Trials 21-30 and 31-40 used 150 microA and 200 microA, respectively, for both the 60-Hz and 3-Hz conditions, to insure that all rats reached the convulsion stage.

A second group of six rats received 60-Hz stimulation on Trial 1 each day. On Trials 2 and 3 the rats were placed in the stimulation apparatus but received no current (60-X-X group). A third group of six rats received three trials of stimulation each day with 60-Hz sine waves (60-60-60 group).

At the end of all experiments, histological analyses were performed on the 20 rats (Gaito, 1976c). After identifying where the tip of each electrode was located, the result was placed in one of four categories: (A) in amygdala, (B) intersection of amygdala and adjacent structure, (C) just outside amygdala, in adjacent structure, (D) outside amygdala, in adjacent structure, but more remote. In previous research we found that most rats with electrodes in structures in Categories A-C convulse within about 30 trials. Thus rats with an electrode in structures indicated by D usually are discarded. In the present experiment only one rat (from the 60-3-3 group) had an electrode in a D structure; the data for this rat were discarded in Experiment 1. The distribution of As, Bs, and Cs in the three groups was about the same.

Table 1
Behavioral Paradigms

Experiment 1: Unilateral Stimulations, Daily Interference	
Group 1	60-3-3, experimentals, n = 8
Group 2	60-X-X, controls, n = 6
Group 3	60-60-60, controls, n = 6
Experiment 2: Bilateral Stimulations, Daily Interference	
Group 1	60-3 alternating sides, experimentals, n = 8
Group 2	60-3 same side, experimentals, n = 6
Group 3	60-60, controls, n = 6
Experiment 3: Unilateral Stimulations, Long-Term Sequential Interference	
Group 1	60-3-60, experimentals, n = 11
Group 2	60-60-60, controls, n = 4
Experiment 3: Bilateral Stimulations, Long-Term Sequential Interference	
Group 1	60-3-60, experimentals, n = 5
Group 2	60-60-60, controls, n = 2
Group 3	60-3 same side, for histology, n = 2
Experiment 4: Unilateral Stimulation, Daily Interference	
Group 1	3-60-3, experimentals, n = 8
Group 2	X-60-X, controls, n = 5
Experiment 5: Unilateral Stimulation, Daily Interference	
Group 1	3-3-60-3-3, experimentals, n = 8
Group 2	X-X-60-X-X, controls, n = 5

Results

Three dependent variables were evaluated by ANOVA procedures: the number of trials to first clonic convulsion (CC), number of convulsions in blocks of 10 trials, and composite score over blocks of 10 trials (Table 2). For the latter, each rat received a value of 1 for Stage 1 behavior, a value of 2 for Stage 2 behavior, and a value of 3 for Stage 3 behavior for each of the 10 trials. The maximum possible composite score for each block was 30; the minimum score was 10.

The first analysis was by a one-factor design. The other dependent variables were analyzed by a partially nested trend analysis (Gaito, 1973); the between-subjects dimension was groups, the within-subjects factor was blocks of trials. There were no significant differences present in any case; however, it should be noted that the

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Table 2
Results of Experiment 1

		Trials			
		1-10	11-20	21-30	31-40
Mean Number of Trials to First CC	60-3-3				19.6
	60-X-X				16.8
	60-60-60				17.0
Mean of Cumulative Number of CCs in Blocks of 10 Trials	60-3-3	0.0	3.3	11.3	20.4
	60-X-X	1.8	7.5	14.7	23.3
	60-60-60	1.5	6.5	14.8	24.0
Mean Cumulative Composite Score*	60-3-3	15.3	36.0	65.0	96.0
	60-X-X	18.7	41.3	68.5	97.2
	60-60-60	18.0	42.8	72.8	102.0

*See text for details.

arithmetic value for the 60-3-3 groups in each of the three variables suggested an inferior mean.

EXPERIMENT 2

Method

In Experiment 1 and in the previous research, all animals had been stimulated unilaterally. In Experiment 2 we were concerned as to whether bilateral stimulation would provide interference in the development of kindling.

Nineteen male Wistar rats (about 140 days of age) were implanted bilaterally with bipolar electrodes in each amygdala. All rats were stimulated 3 times/day. Eight rats were stimulated simultaneously with 60-Hz sine waves on one side and 3-Hz sine waves on the other side on Trial 1. On the next trial, the 60 and 3 Hz were interchanged. These eight rats were the 60-3 alternating pattern group (Table 1).

A second group of six rats received 60-Hz stimulation on one side and 3-Hz stimulation on the other. On every trial the 60-Hz stimulation was to the same side, as was the case with 3-Hz stimulation. This was the 60-3 same side group. A third group was stimulated with 60-Hz sine waves to both amygdalae on every trial (60-60 group).

Stimulation with 3 Hz and 60 Hz was at an intensity of 100 microA during the first 30 trials. Trials 31-40 used 150 microA; 200 microA was the intensity for Trials 41-50 to insure that all rats reached the convulsion stage.

At the end of all experiments, histological analyses were performed on these rats. No data were discarded; all electrode tips were in structures indicated by Categories A-C.

Results

The three dependent variables used in Experiment 1 were evaluated for the bilateral rats. A partially nested ANOVA trend analysis (Gaito, 1973) was used for the composite score and for the number of CCs in blocks of 10 trials; a one-factor design was employed for the other dependent variable. For the analyses over block of trials, a significant trials effect results inasmuch as scores increase over trials. However, this trend analysis provides an efficient and powerful method of evaluating the possible differences between the curves for the three groups over trials. The important source of variation was the interaction of groups with trials, with the emphasis on the regression components, namely, linear, quadratic, cubic, and quartic. The first component was the only one that was significant, which indicated that the linear components of the three curves were different [$F(2,15) = 8.31$, $p < .01$]. To identify specific differences, trend analyses were used that were equivalent to multiple comparisons for qualitative categories. The 60-60 group was shown to be significantly different from the combination of the two other groups in the linear component [$F(1,16) = 7.54$, $p < .05$]. The 60-3 alternating group was inferior to the 60-3 same side group [$F(1,16) = 9.08$, $p < .01$]. The 60-60 group was not significantly different from the 60-3 same side group [$F(1,16) < 1$, $p > .05$].

Table 3 indicates that after 10 trials the three groups show identical behavior. However, by 20 trials the three groups begin to diverge and the divergence increases thereafter; for example, the 60-60 group has the greatest, and the 60-3 alternating group the smallest mean number of CCs.

In the other analyses no significant differences were present. However, in each case, according to the arithmetic mean, there was some suggestion that the performance of the 60-60 group was superior to the other groups and the 60-3 same side group was superior to the 60-3 alternating group, but that the "noise" level was obscuring the superiority.

EXPERIMENT 3

Method

As soon as 40 trials had been completed with the third group of six rats in Experiment 1 (60-60-60 group), these rats were stimulated to 60 convulsions. During the last six trials, the lowest intensity required to trigger a convulsion was determined and 15 microA was added (to handle day-to-day fluctuations). This intensity was the effective threshold intensity (ETI).

Four of these rats were stimulated for 36 trials over 12 days with 3-Hz sine waves at double the ETI (experimentals). The other two received 36 further trials of 60-Hz brain stimulation at the determined ETI (controls). Then all rats were subjected to six or more test trials with 60-Hz sine waves at the ETI. If a rat convulsed on the six trials, no further stimulation was involved. If convulsive behavior did not occur in nine trials, the intensity was increased to determine the new ETI required to produce a convulsion. After approximately six convulsive trials showing a stable pattern of convulsing, the ETI was decreased gradually over a number of trials in an attempt to lead the rat back to its previous level of responding. The last six trials were with the original ETI to determine if the rat had returned to its previous level of behavior. Many of the rats received 30 to 33 test trials (10-11 days).

Nine other bilateral stimulation rats from Experiment 2 that showed a pattern of convulsions indicating that the convulsion was resulting from stimulation of only one side were treated in a similar fashion to these six rats. There were seven experimental and two control rats. Thus, over the two sets of animals, there were 11 rats that constituted the 60-3-60 group and 4 that were in the 60-60-60 group.

The five bilateral rats from the 60-60 group in Experiment 2, plus two others that were showing convulsions in response to stimulation on both sides, were treated in a similar fashion to the unilateral experimentals and controls, except that stimula-

Table 3
Results of Experiment 2

		Trials				
		1-10	11-20	21-30	31-40	41-50
Mean Number of Trials to First CC	60-3-A					33.9
	60-3-S					26.5
	60-60					21.2
Mean of Cumulative Number of CCs in Blocks of 10 Trials	60-3-A	0.0	.5	2.1	4.8	7.8
	60-3-S	.5	3.2	5.5	16.0	24.3
	60-60	.2	4.8	10.8	19.0	29.4
Mean Cumulative Composite Score*	60-3-A	15.5	34.0	54.7	74.3	98.1
	60-3-S	17.2	38.2	61.5	86.0	116.0
	60-60	17.4	40.8	66.8	94.8	124.8

Note—*A = alternating, S = same.* **See text for details.*

tion on each trial was of bilateral nature. There were five experimentals and two controls.

Two other rats from the 60-3 same side group from Experiment 2 were stimulated bilaterally as in Experiment 2 to 130 convulsions; these two rats were for histological purposes to contrast the site of electrode points for 3-Hz stimulation with that for 60-Hz stimulation. One side always received 3-Hz stimulation; the other side was stimulated with 60-Hz sine waves. No difference in the tissue around electrode tips was apparent.

Results

The results are shown in Table 4. Not a single rat of the 16 (11 unilateral and 5 bilateral) convulsed on Trial 1. One unilateral rat convulsed on Trial 2 and one on Trial 3. All other rats would be considered to be showing the "reversal effect." Thus, 9 unilateral and 5 bilateral rats or 14 of the 16 indicate the reversal tendency. On the other hand, all control rats convulsed on Test Trial 1.

In the previous experiments, there was a tendency for latencies to convulsions to increase after stimulation with 3-Hz stimulation. Similar results occurred in Experiment 3. There were a greater number of rats showing increments than rats that had decrements for both unilateral and bilateral groups. As before, all rats subjected to 60-Hz stimulation over all trials had decreased latencies. Thus, it seems that 3-Hz brain stimulation tends to increase latencies, whereas 60-Hz stimulation brings about decrements.

A rest group might have been used in Experiment 3 to preclude the possibility that the reversal effect was due to a rest period in which no convulsions occurred, but it was deemed unnecessary. Although some reduction in the convulsive tendency occurs with some rats after 56 days (McIntyre & Goddard, 1973), at 3 months (Goddard et al., 1969), and after 6 months (Gaito, 1976a), there is no significant decrement for intervals up to 6 weeks (Gaito, 1976a; Goddard et al., 1969; McIntyre & Goddard, 1973). Even for the 3- and 6-month periods, rats tend to convulse on the first trial or within a few trials; a great number of nonconvulsion trials as observed in Experiment 3 do not occur. Furthermore, in the previous experiments (Gaito, 1979), a few rats were used as resting controls for 12, 20, and 22 days; these rats convulsed on all test trials.

To check further on this aspect, two of the unilateral control rats from Experiment 3 rested for 12 days (the equivalent of 36 trials with 3-Hz stimulation). Then each was stimulated for six trials at the same intensity as had been used on the last 60-Hz stimulation trials. Both rats convulsed on each of the six trials. This result confirmed our previous conclusion that a rest group was not necessary.

Table 4
Results of Experiment 3

Rat	LP	LT	DP	DT	1st CC	ETI_1	ETI_2	2nd ETI_1
Unilateral Stimulation: Experimentals								
15	3.7	14.0	31.0	29.8	11	42	154	No
17	12.7	15.2	20.3	22.8	10	70	182	No
18	1.7	3.4	21.8	34.4	10	64	84	16
19	8.7	8.8	17.8	23.2	10	112	154	No
21	10.0	9.8	22.0	23.8	2	126	126	2
24	7.8	13.2	14.0	28.0	9	56	56	9
25	9.3	17.2	14.7	26.8	13	168	560	No
26	4.3	5.0	33.7	33.4	10	70	112	25
27	11.8	10.4	20.5	32.2	10	84	140	No
29	7.0	15.4	23.8	25.6	3	56	56	3
30	16.8	14.0	22.2	23.0	10	84	140	No
Unilateral Stimulation: Controls								
16	10.8	5.5	18.7	30.2	1	98	98	1
20	13.0	7.0	22.7	19.3	1	126	126	1
22	13.2	6.7	17.8	19.3	1	112	112	1
34	14.8	4.8	24.3	32.0	1	196	196	1
Bilateral Stimulation: Experimentals								
28	11.0	16.7	25.2	35.7	5	84	84	5
37	9.0	8.2	20.2	21.4	13	98	98	24
38	10.2	11.6	20.5	23.0	11	98	476	No
39	5.7	14.6	28.5	25.0	14	84	336	No
40	5.7	7.8	23.0	22.6	11	56	126	No
Bilateral Stimulation: Controls—60-3								
31	2.7	1.3	23.5	23.2	1	140	140	1
32	12.5	7.2	30.7	16.7	1	126	126	1
Bilateral Stimulation: Controls—60-60								
23	10.0	5.8	14.2	20.3	1	126	126	1
36	5.0	2.0	27.7	24.5	1	224	224	1

Note—LP and DP = the mean latency and duration values of the last 6 CCs prior to stimulation with 3 Hz: LT and DT = the mean latency and duration for CCs during the test trials; "1st CC" = trial of the first CC; "2nd ETI_1" = test trial back to ETI_1.

EXPERIMENT 4

Method

One reason why 3-Hz stimulation was not effective for the 60-3-3 group in Experiment 1 might be that the intensity was too great. Thus Experiment 4 was conducted to check on this aspect. The eight rats that had been exposed to 60-3-3 stimulation in Experiment 1 were brought to the CC stage and then had the ETI determined over six trials. Then they received 10 days of stimulation. Trials 1 and 3 each day were by 3-Hz sine waves. Trial 2 was 60-Hz stimulation (experimentals: 3-60-3 group). The six rats from Experiment 1 that had one 60-Hz trial per day and two nonstimulation had the ETI determined over six convulsion trials after reaching the CC stage. One rat had to be discarded because a stable ETI could not be obtained. This group then received 10 days of stimulation. Trial 2 was the same as for the eight experimentals. However, on Trials 1 and 3 each day, the rat was placed in the stimulation apparatus but received no current (controls: X-60-X group).

Results

The 3-Hz stimulation before and after stimulation with 60-Hz sine waves produced a 50% suppressive effect, an effect that was significant in a one-factor ANOVA [$F(1,11) = 9.01$, $p < .025$]. The mean number of convulsions in 10 trials was 5.0 and 10.0 for experimentals and controls, respectively.

EXPERIMENT 5

Method

Inasmuch as 3-Hz stimulation before and after the 60-Hz stimulation was successful in suppressing the convulsive tendency by 50%, more trials of 3-Hz stimulation daily might produce greater suppression. Experimental rats received one more trial before and after the 60-Hz stimulation (3-3-60-3-3 group). The controls also received one more trial of placement in the apparatus before and after the 60-Hz trial (X-X-60-X-X).

Results

The added trials produced greater suppression. Only 19% of the total possible convulsions resulted. A subjects by treatments ANOVA over the two sets of 10 trials with the experimentals in Experiments 4 and 5 (3-60-3 vs. 3-3-60-3-3) indicated that these differences were significant [$F(1,7) = 9.09$, $p < .05$]. The mean number of convulsions in 10 trials was 1.9 and 10.0 for experi-

mentals and controls, respectively, in Experiment 5.

Apparently, the 3-Hz stimulation increases the ETI required to elicit a convulsion, whereas 60-Hz stimulation tends to decrease it. This aspect was checked with the eight experimentals and five controls after the completion of Experiment 5. The intensity of stimulation with 60 Hz was increased slowly on one trial with each of these 13 rats; all rats convulsed on this trial. No change in ETI occurred with one experimental rat that had convulsed on every trial in Experiments 4 and 5. Presumably, the opposite tendencies of 3-Hz and 60-Hz stimulation were in equilibrium for this animal. Each of the other seven experimental rats required an increase in ETI, with the mean increase equal to 115 microA; the range was from 84 to 252 microA.

Each of the five control rats had a decrease in ETI. The mean decrease was 26 microA, and the range was from 8 to 45 microA. Thus, these results seem to show that 3-Hz and 60-Hz stimulation work in contradiction to each other.

Each rat was stimulated with 60-Hz sine waves for five more trials to determine if the ETI was stable. The ETI was stable for the five control rats and the one experimental animal that had convulsed on every trial in Experiments 4 and 5. However, each of the other seven rats required an increase in intensity to elicit a convulsion.[1]

GENERAL DISCUSSION

The 3-Hz stimulation did not produce consistent statistically significant interference effects relative to the convulsive tendency in Experiments 1 and 2. However, In Experiment 2 there were significant differences in the composite score analysis, with the 60-3 alternating group showing the poorest performance over the 50 trials. The arithmetic mean for the 60-60 group was superior to that of the other groups in other analyses also, although these differences were not statistically significant. Likewise, in Experiment 1 the arithmetic mean for the 60-X-X group was superior to that of the 60-3-3 group in two of the three analyses, even though significant differences did not occur. Furthermore, the 3-Hz suppressive potential appears to be present when one considers the results of Experiments 3-5. Apparently, the intensity used in the first two experiments was too great for the 3-Hz stimulation effects to be exerted consistently. The results of Experiments 3-5 seem to indicate that 3-Hz stimulation increases the ETI, whereas 60-Hz stimulation decreases it.

The reversal effect, or "suppression effect," observed in Experiments 3-5 is consistent with the results observed in previous research (Gaito, 1979). These results seem to show that 3-Hz brain stimulation produces brain events that interact in some way with those effected by 60-Hz stimulation in bringing about the convulsive state. Such results would seem to have important theoretical implications relative to brain function, as well as suggesting possible therapeutic results in some types of epilepsy (e.g., focal epilepsy).

The exact basis for the 3-Hz effect is not clear at this time. The results appear not to be due to lesions at the site of stimulation. If lesions were the basis for the effect, none of the rats would convulse at the previous ETI, whereas our results indicate that some rats can return to this level within at least 33 trials. Histological analyses also suggested that lesions are not precipitated by 3-Hz stimulation. The tissue in the area of electrode tips appears the same for both 3-Hz and 60-Hz stimulation sites. Inasmuch as Douglas and Goddard (1975) reported results suggesting that 60-Hz stimulation produces the convulsion state by synaptic changes, it might be that 3-Hz stimulation interferes with these synaptic changes, or possibly it sets up antagonistic synaptic changes.

Burnham (1975) suggested that the kindling effect consisted of the development of a convulsion mechanism and the use of a triggering mechanism. In this framework one would say that the effect of 3-Hz stimulation is on the triggering mechanism, inasmuch as all 13 rats convulsed on one trial after Experiment 5. If an effect on the convulsion mechanism were involved, one would expect that a number of trials would be required to precipitate a convulsion. However, it is possible that the major effect is on the triggering mechanism, but that some effect might result to the convulsion mechanism, especially if 3-Hz stimulation were continued for long periods of time.

The effect of 3-Hz stimulation may be a relatively permanent one, or at least moderately so. In Experiment 3 test trials were conducted for up to 11 days after termination of 3-Hz stimulation trials. Some rats still had not convulsed in response to stimulation at an intensity that had effected a convulsion previously. Also, Experiments 3-5 were conducted over a period of approximately 1 month, and increases in ETI occurred for some rats.

The effect of 3-Hz stimulation appears to be twofold in nature. First, there is probably a short-term effect in which the brain events act within hours or 1 or 2 days to produce mild interference effects relative to 60-Hz stimulation brain events. Then there is a more long-term effect that cumulates over time. This aspect is best exemplified by the fact that in Experiments 3-5, some rats had two increases in ETI. There were three determinations of ETI, and for some rats the following result occurred: $ETI_3 > ETI_2 > ETI_1$. Approximately 30 days intervened between the determinations of ETI_1 and ETI_3.

The present results and those of previous research suggest that there are four "signs" that accompany the reversal effect. The signs are (1) no CCs on early test trials (this is the most important of the signs), (2) increase in latencies, (3) increase in ETI, and (4) unstable ETI. One or more of these signs are present with each rat that shows 3-Hz interference effects. On the other hand, it is interesting to note that rats that do not show interference tendencies tend to have low and stable ETIs and a low latency. The low ETI and low latency appear to offer resistance to the development of the tendency. Obviously, these suggestions are of tentative nature. Further research is required to evaluate the signs and the 3-Hz interference effects.

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NOTE

1. To check further on the stability of the ETI, and to investigate 3-Hz/60-Hz time intervals, 12 of the 13 rats used in Experiments 4 and 5 and 2 controls from Experiment 3 were given 12 stimulation trials with 60 Hz. For two of these rats, only 60-Hz stimulation occurred. The other 12 rats received 3-Hz stimulation; 2 rats each were stimulated with 3-Hz sine waves 0, 2, 5, 10, 15, and 30 min before the 60-Hz stimulation was applied. Then all rats received six more test trials with 60 Hz only. The two rats that received only 60-Hz stimulation convulsed on every trial. There appeared to be no real difference between the intervals; one or both rats showed 3-Hz interference at all intervals. Only three rats convulsed on each of the 12 trials. The other nine rats had one to six convulsions in the 12 trials. However, only one rat did not show a convulsion on Trial 1. Four of the five rats that convulsed on all 12 trials had a slight decrease in ETI on the last six trials. The fifth rat had no change in ETI. Only one of the other nine rats had a stable ETI; the other eight required an increase in ETI to elicit a convulsion.

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