High-intensity septal ICS depressed the prestimulus heart level (see Fig. 1). With septal stimulation, then, either high intensity or fast repetition rate lowers prestimulus heart rate ("background levels"). The effect of repetition rate was verified by the finding that for all intervals shorter than 20 seconds, each of the four rats showed progressively decreasing prestimulus heart rate levels as rate of stimulation increased.

This third study seems to begin to resolve the contradiction between the results of our first two experiments and Malmo's results. One source of the difficulty is temporal: the early effect of septal ICS is accelerative, but the late effect is pronouncedly decelerative. However, at rates of septal stimulation that would be achieved during bar-pressing, we observed only an accelerative phasic component which was superimposed upon a diminished overall heart rate level (tonic effect). With hypothalamic stimulation, moreover, which is generally regarded as more reinforcing, the accelerative component was superimposed on a heart level that either did not change or increased. These facts make it impossible for us to accept a linkage between the reinforcing properties of ICS and a "parasympathetic or quieting effect." Indeed, the polyphasic nature of the responses, both to septal and hypothalamic stimuli, makes it difficult to characterize the autonomic participation in the reinforcement process as exclusively "parasympathetic" or "sympathetic" (*7*).

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7. Supported by grants M-623 (J.I.L.) and M-4529 (E.S.V.) from the National Institute of Mental Health. W.J.M. is a U.S. Public Health Service postdoctoral fellow (MF-8687).

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Heart Rate: Differential Effects of Hypothalamic and Septal Self-Stimulation

Abstract. *Heart rate in rats was recorded during self-stimulation with electrodes permanently implanted in both the hypothalamus and the septal region. Acceleration was observed during stimulation of the hypothalamus, and deceleration during stimulation of the septal region. In both areas self-stimulation reduced variability in heart rate.*

Malmo (*1*) suggests a relationship between the reinforcing properties of self-stimulation of the septal region and a parasympathetic "quieting" effect indicated by cardiac deceleration after stimulation. Our study compares the cardiac changes during self-stimulation of the septal region with such changes during self-stimulation at other "rewarding" brain sites (for example, hypothalamus) in the same animal.

Two enameled, stainless steel, bipolar electrodes were stereotaxically implanted (one in the septal region and one in the hypothalamus) in ten male albino rats approximately 120 days old, according to an established procedure (*2*). Four days after the operation all animals were trained to press a lever for brain stimulation. The experimental space consisted of a box, 12 by 12 by 14 inches, equipped with a microswitch actuated by a lever. A white light was positioned directly above the manipulandum. Brain stimulation resulted only when the white light was on. The electrical stimulus consisted of a bidirectional rectangular waveform (0.2 msec pulse duration) at a frequency of 100 cy/sec. The pulse train produced by a press of the lever lasted for 0.5 second. Current levels were determined individually for each animal within the following limits: 0.7 to 1.0 ma in the septal region, 0.2 to 0.5 ma in the hypothalamus.

Five rats were trained daily for 1 hour with septal self-stimulation, and this was followed later by daily training with hypothalamic self-stimulation. In the remaining five rats the procedure was reversed. Each session consisted of 5-minute periods of self-stimulation (light "on") alternating with 5-minute periods of "time-out" (light "off") when pressing the lever produced no self-stimulation. Lever responses were recorded separately for each on and off interval. Heart rate was recorded continuously with tantalum disk electrodes (1.5 cm in diameter, 1.0 mm thick) taped to the animals' side over the thoracic region. This method yielded polygraph tracings free from artifacts from which heart rate was determined by a count of the *R* waves in the electrocardiogram during each 20-second interval throughout both self-stimulation and timeout periods. Ectopic beats, randomly distributed throughout the stimulation and time-out periods, were not included in the heart-rate analysis.

Histological verification of placement of the electrodes was obtained after the experiments.

The results obtained with both hypothalamic and septal self-stimulation are summarized in Table 1. The data represent mean heart rate and lever-pressing values determined during one 50- to 70-minute session for each placement according to the alternating 5-minute on, 5-minute off procedure. Eight of the ten rats maintained stable lever-pressing rates for hypothalamic self-stimulation and nine of the ten animals responded consistently for septal self-stimulation. A comparison of the 5-minute alternating control and

Table 1. Mean heart rates and lever-pressing rates for each animal during experimental sessions involving self-stimulation in the hypothalamus and in the septal region.

Animal No.	Heart rate (beats per minute)		Lever-pressing rate (responses per minute)	
	Control	Self-stimulation	Control	Self-stimulation
	Hypothalamus			
1	359.8	428.2	0.6	43.8
2	409.5	424.6	1.6	47.9
3	322.6	352.2	1.5	13.0
4	349.6	469.8	1.6	28.0
5	457.9	464.3	2.0	39.4
6	477.7	486.1	2.1	40.7
7	438.5	413.6	2.3	24.3
9	490.0	464.0	2.1	21.6
	Septal region			
1	429.1	401.9	0.8	33.0
2	407.3	347.8	0.7	32.7
3	379.1	356.2	0.1	38.0
4	383.4	343.9	0.5	16.4
5	404.9	384.5	2.5	7.8
6	446.9	445.9	1.5	33.8
7	391.7	399.3	1.1	25.1
8	382.3	362.6	0.1	31.8
10	401.2	383.2	0.2	33.5

self-stimulation periods for the hypothalamic placement revealed acceleration in heart rate for six of the eight animals during self-stimulation. The remaining two animals performed in a stable manner for hypothalamic self-stimulation and showed a decrease in heart rate during the 5-minute self-stimulation periods compared to the 5-minute control periods. For septal self-stimulation these animals showed sharply contrasting results. A comparison of the 5-minute alternating control and self-stimulation periods during such septal stimulation sessions revealed a deceleration in heart rate for eight of the nine animals during self-stimulation. The ninth animal performed in a stable manner but showed an increase in heart rate. The differences in heart rate for the two kinds of self-stimulation were highly significant. A Friedman two-way analysis of variance (*3*) provided statistical confirmation ($p = .001$).

A further analysis of the data for all 17 electrodes (both in the hypothalamus and in the septal region) showed that the range of variation in heart rate was consistently lower during the 5-minute self-stimulation period than it was in the alternating 5-minute control periods. In 15 of the 17 electrode placements producing self-stimulation, variability of the cardiac rate decreased regardless of the direction of the rate change or its magnitude. Although the lever-pressing response rates were higher for hypothalamic than for the septal self-stimulation, no systematic relationship between the lever-pressing response rate and the variability in heart rate could be observed. In addition, it seems improbable that the reduction in heart-rate variability can be easily explained by changes induced by the lever-pressing behavior per se, since previous experiments (*4*) have indicated that muscular activity actually produces increases in the variability of the heart rate. Direct activation of neurohumoral mechanisms by the brain stimulation, however, could account for such effects upon the peripheral reactivity of the heart.

Histological analysis (*5*) of the hypothalamic electrode placements producing cardiac acceleration revealed involvement of the dorsomedial and ventromedial nuclei. The two hypothalamic electrode placements which produced cardiac deceleration involved the dorsal hypothalamus. One of these placements was medial to the fornix, and the second impinged upon the ventricle in the region of the lateral septal nucleus. Septal electrode placements which produced cardiac deceleration were located in the rostral and medial septal nuclei. The one septal electrode placement which produced cardiac acceleration involved the lateral septal nucleus bordering on the nucleus accumbens septi.

The effects of electrical self-stimulation of the brain on heart rate vary markedly with the location of the electrode in the brain. Our findings on the slowing of heart rate during septal self-stimulation are in substantial agreement with Malmo's results despite the difference in methods of measurement in the two experiments. On the other hand, our findings on heart-rate acceleration during hypothalamic self-stimulation make it difficult to accept general propositions which relate the rewarding effects of brain stimulation to parasympathetic quieting reactions of the autonomic nervous system; moreover, oversimplified interpretations of the role of sympathetic and parasympathetic influences on the rewarding effects of brain stimulation which are based solely on heart rate changes may be somewhat premature without more information about neurohumoral and hemodynamic factors which can affect cardiovascular function.

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Seed Discharge in Arceuthobium: A Photographic Study

Abstract. *Photographs, made at a speed of 5 microseconds, of the ejection of the* Arceuthobium *seed from its fruit, show that tumbling in the vertical plane begins soon after discharge and that most seeds have turned 90 degrees when they have traveled about 6 centimeters. As the seeds leave the fruit they have a viscous sheath around the trailing end that disintegrates after the seeds have traveled about 2 to 3 centimeters. This viscous material does not act as a rudder as has been postulated.*

The seed dispersal mechanism of the dwarfmistletoe (*Arceuthobium*) is unique and has been considered by Ridley (*1*) to be one of the most efficient in the whole plant kingdom. The general mechanics of seed expulsion are known, but specific processes and forces are far from understood (*2, 3*). Each *Arceuthobium* fruit contains a single semifusiform seed (Fig. 1). When the fruit is ripe, the pedicel is elongated and recurved so that the distal end points downward. An abscission zone develops between the tip of the pedicel and the base of the fruit. High hydrostatic pressure develops in a layer of viscin cells surrounding the seed, and when the fruit is severed from the pedicel, the exocarp of the fruit rapidly contracts and hurls the seed upward.

The greatest horizontal distance (for seed flight to a point on the same level as the point of discharge) that we have measured was 1463 cm (48.0 feet) for *Arceuthobium vaginatum* f. *cryptopodum*. Weir (*4*) recorded a flight of 66 feet from a point 8 feet above ground level for an unnamed species of *Arceuthobium*.

Hawksworth (*3*) studied the ballistics of seeds of *A. vaginatum* f. *cryptopodum*, and estimated their initial velocity to be about 1370 cm/sec and the initial acceleration to be 4.7×10^6 cm/sec^2.

In an attempt to learn more of the expulsion process, seed discharge was studied photographically. The equip-

Table 1. Vertical departure of seeds of *Arceuthobium* from original line of flight.

Flight distance (cm)	Seeds measured (No.)	Vertical angle of departure (mean and S.D.) (deg)
0.6 to 1.5	7	17 ± 17
1.6 to 2.5	63	29 ± 29
2.6 to 3.5	36	45 ± 39
3.6 to 4.5	8	63 ± 55