

17. These increases in catecholamine levels in immature rat brain after treatment with L-dopa are consistent with previous reports: C. Kellogg and P. Lundborg, *Psychopharmacologia* **25**, 187 (1972); J. T. Coyle, in *Dynamics of Degeneration and Growth in Neurons*, K. Fuxe, L. Olson, and Y. Zotterman, Eds. (Pergamon, Oxford, England, 1974), pp. 425-434.
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- 19a. *Note added in proof:* That this possibility merits consideration is supported by recent studies demonstrating that sympathetic neurons in culture may synthesize, take up, and store different neurotransmitters at successive stages of development, dependent upon the culture conditions [M. Johnson, D. Ross, M. Meyers, R. Bunge, *Neurosci. Abstr.* **II**, 766 (1976); S. Landis, *Proc. Natl. Acad. Sci. U.S.A.* **73**, 4220 (1976); L. Reichert, P. Patterson, L. Chun, *Neurosci. Abstr.* **II**, 225 (1976)]. However, preliminary results from our laboratory reveal that the SGV synapses in immature neocortex are not derived from intrinsic or thalamic neurons since they are significantly decreased after brainstem lesions of the ascending noradrenergic axons (N. Zecevic and M. E. Molliver, in preparation).
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Trigeminal Substrates of Intracranial Self-Stimulation in the Brainstem

Abstract. *Intracranial self-stimulation was elicited by electrodes located in the trigeminal motor nucleus of the rat. Rebound jaw movements were also elicited at positive self-stimulation placements, but control experiments revealed that the lever pressing was not a motor artifact. It is suggested that modulation of trigeminal motoneurons may serve as an important reinforcement mechanism in the brainstem.*

Intracranial self-stimulation (ICSS) at sites in the pontine region of the brainstem has been attributed to excitation of noradrenergic neurons located in the locus coeruleus (LC) (1-3). This hypothesis has been challenged recently by a number of experiments in which both whole brain depletion of noradrenaline (4) and localized neurotoxic (5) and electrolytic (6) lesions of the noradrenergic dorsal tegmental bundle ascending from the LC failed to disrupt ICSS in the LC. In the original mapping study that implicated the LC in ICSS, the investigators emphasized that repetitive jaw movements were an excellent indicator of positive placements and cautioned that one could not rule out the involvement of the trigeminal system in pontine ICSS (1). These observations are supported by the preponderance of oral rather than locomotor behavior elicited by electrical stimulation in the dorsal pontine area (7). We have now confirmed a trigeminal substrate of brain stimulation reward by showing that both ICSS and repetitive

oral behavior are elicited from electrode placements in and immediately dorsal to the motor nucleus of the trigeminal nerve (Mot V).

The mesencephalic nucleus of the trigeminal nerve (Mes V) is situated lateral to and intermingled with the LC in the dorsal pontine tegmentum (8). This nucleus is comprised of neurons that innervate the masticatory muscles and whose central axons establish bilateral (9), monosynaptic (10), excitatory (11) connections with masticatory motoneurons in Mot V. An analysis of histological data from several studies of ICSS in the dorsal pons reveals many positive placements in Mes V (1, 3, 5, 12). Furthermore, placements in the LC are in such close proximity to this nucleus that its neurons could easily be influenced by current spread. If Mes V mediates ICSS and stimulation-bound oral behavior, then electrical stimulation of its terminal projections in Mot V should also provide positive reinforcement. Accordingly, we mapped the region of the brainstem in

which Mot V is located for ICSS and stimulation-bound behavior (SBB).

Male Wistar rats, in which small-diameter (125 μ m) bipolar electrodes had been stereotactically implanted were tested for ICSS in five Plexiglas Skinner boxes (13). Animals were trained in daily 30-minute sessions to bar-press for brain stimulation. During the first 15 minutes of six daily test sessions, the experimenter "shaped" the bar-pressing response by initially reinforcing orientation to the manipulandum and later by rewarding contacts with the bar. In the second 15-minute period, spontaneous bar-presses were recorded. Those rats attaining a criterion of at least 50 spontaneous responses in 15 minutes on test day 7 were classified as having a positive ICSS placement. On completion of behavioral testing, each brain was prepared for histological analysis (14). Of the 66 placements, 29 supported ICSS; positive placements were located throughout and dorsal to Mot V (Fig. 1). Negative placements were found ventral to Mot V, laterally in the main sensory trigeminal nucleus, and medially in a region that would coincide with the ascending trajectory of both the noradrenergic central tegmental tract (15) and the adrenergic axon bundle (16). The mean of the responses at positive sites (per 15-minute period) was 148, and the current intensities employed ranged from 15 to 50 μ A (\bar{X} = 35 μ A). In contrast, the mean rate obtained on test day 7 by animals with ineffective placements was 8, and by an unstimulated control group, 8.

If the trigeminal system plays an important role in brainstem ICSS, it is important to consider its relationship with other ICSS sites in the pons and medulla. The connection between Mes V and Mot V has already been emphasized. Preliminary unpublished observations appear to rule out involvement of the LC, as bilateral destruction of this nucleus by electrolytic lesions had no effect on ICSS in Mot V. Another important site for ICSS is located caudal to Mot V, in a region ventral to the solitary nucleus (17); this region is also innervated by the tract of Mes V (10). Stimulation of this area would produce antidromic excitation of trigeminal motoneurons; not surprisingly, jaw movements are an excellent predictor of ICSS at this site. Positive ICSS placements dorsal to Mot V (Fig. 1) may reflect activation of the intertrigeminal commissural pathway (18), which projects bilaterally to Mot V and the parvocellular reticular formation.

As a control for the possibility that bar-pressing was an artifact of biting elicited by stimulation of Mot V, the pattern

of responding for two animals with high ICSS rates was graphed for 1 hour on a cumulative recorder. No spaced bursts of responding were observed, as would be predicted by an explanation in terms of a motor artifact, whereas constant lever-pressing was observed throughout the session. A second control was obtained by training animals to perform a different operant response in which performance would not be facilitated by biting. In this situation animals readily acquired a nose-poke response when electrical stimulation was made contingent upon this behavior. The mean response rate in this situation was 436 (in 30 minutes) as compared to 79 with no brain stimulation.

After completion of the ICSS tests, those animals ($N = 54$) with secure electrode assemblies, who were not tested in the nose-poking task, were carefully screened for SBB. A high incidence of elicited oral behavior at positive ICSS placements would provide further support for the involvement of the trigeminal system in brainstem ICSS. Animals were tested for SBB on 3 days, each daily session consisting of ten 30-second periods of continuous electrical stimulation (7 to 150 μ a) alternating with an equal number of periods of the same

duration in which there was no stimulation. The data presented in the bottom panel of Fig. 1 are summaries of in vacuo oral behaviors elicited during the ten stimulation periods and ten interstimulation intervals (ISI) on the final day of testing for SBB.

The relationship between ICSS and SBB is shown in the upper and lower sections of Fig. 1. Each symbol in the lower section represents the class of SBB observed after stimulation of a specific ICSS site located at the same coordinates as shown in the upper section of Fig. 1. The predominant category of behavior observed during the SBB tests was jaw movements of large amplitude beginning shortly after the termination of brain stimulation and, in several cases, continuing for the complete 30-second ISI. Brief periods of teeth chattering were also seen occasionally. Of the 25 placements from which oral behavior was elicited during the ISI, 18 supported ICSS. This category included almost all of the placements located directly in Mot V. Nine animals displayed jaw movements in both stimulation and ISI periods, and four had positive ICSS placements. Another nine subjects, all of which had negative ICSS placements, displayed oral behavior only during the

stimulation period. There were 11 electrodes from which no oral behaviors were observed during SBB tests; none of these electrodes supported ICSS. The majority of these placements were located medial to Mot V, and a few elicited locomotor escape responses were recorded. Locomotor responses were not observed at any other electrode loci, nor was stimulation-induced feeding, drinking, or gnawing.

Clearly, the best predictor of ICSS in the Mot V area is jaw movement during the ISI. All of the animals with positive ICSS placements showed such movements, and a minority also displayed oral behavior during the stimulation period. The ISI jaw movements can be attributed to rebound release from inhibition produced by activation of inhibitory synapses on the trigeminal motoneurons (19). As such, this rebound behavior contrasts with that accompanying excitation of trigeminal motoneurons after stimulation of Mes V (11). In the latter instance, stimulation-induced oral behaviors do not extend into the ISI (7).

Recently, trigeminal deafferentation has been shown to disrupt both the motivational and sensorimotor mechanisms involved in feeding (20). It has been suggested that these functions may normally

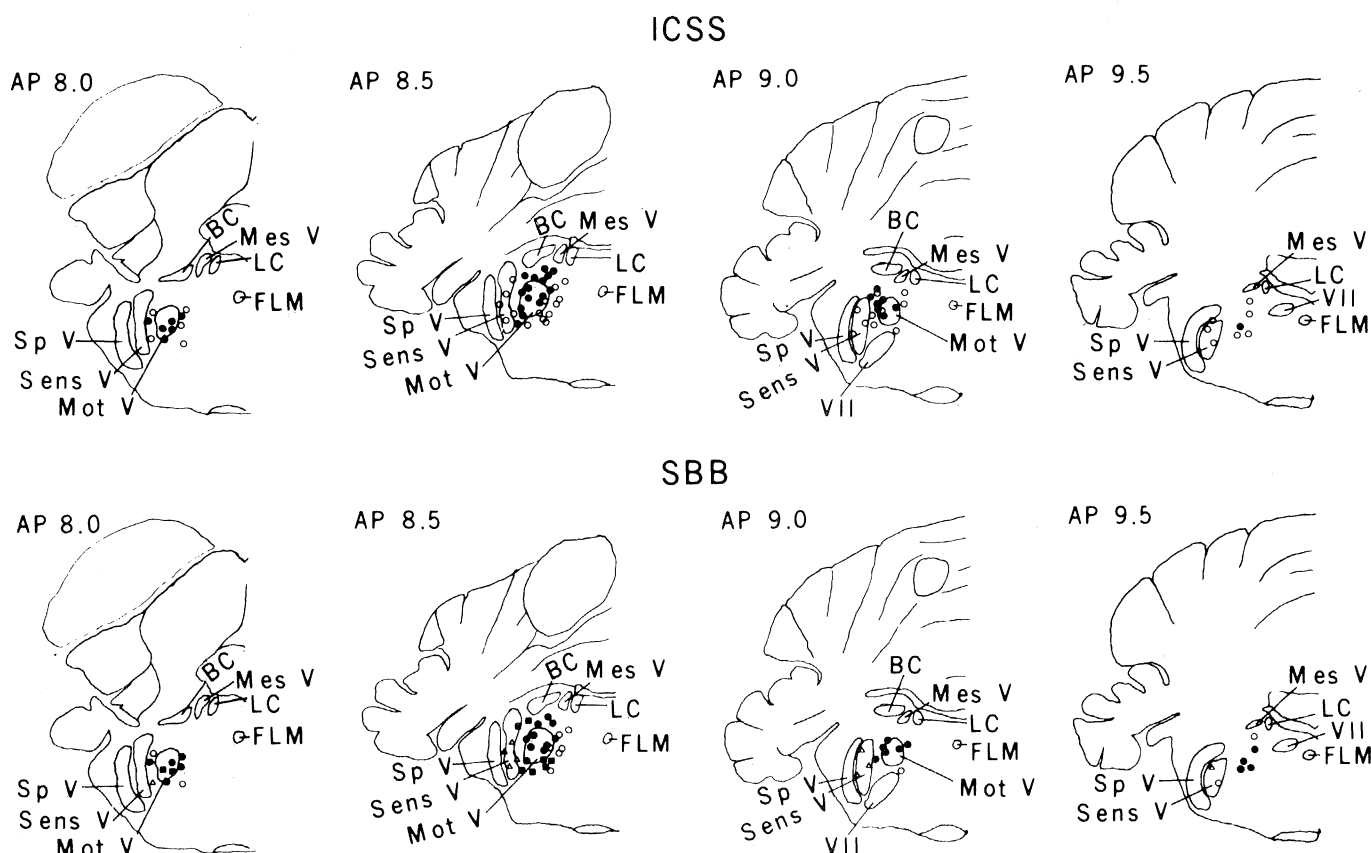


Fig. 1. (Top) Distribution of electrode placements positive (●) and negative (○) for ICSS on redrawn sections of the brainstem (23). Numbers to the upper left of each section indicate distance posterior to bregma in millimeters. Abbreviations: BC, brachium conjunctivum; LC, locus coeruleus; FLM, fasciculus longitudinalis medialis; SpV, spinal tract of the trigeminal nerve; Sens V, main sensory nucleus of the trigeminal nerve; VII, facial nerve. (Bottom) Classification of stimulation-bound behaviors (SBB) elicited from ICSS sites shown in top panel: no oral behavior (○), oral behavior during the stimulation period (△), interstimulation interval oral behavior (●), oral behavior during both periods (■).

be mediated by connections between trigeminal afferents and neurons that directly control feeding. Given the high correlation between brain stimulation reward and the jaw movements we observed after stimulation ceased, it is possible that the increased modulation of trigeminal motoneurons (which facilitates chewing behavior) is related to the positive reinforcement associated with feeding. As such, this suggestion is consistent with response-oriented theories of reinforcement (21), in which reinforcement is thought to be isomorphic with the facilitation of the neural systems underlying species-specific motor behaviors. These theories in turn have received further support from the finding that stimulation of other important motor systems, specifically the extrapyramidal system (22), and cerebellum (23), supports ICSS.

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14. Frozen sections of each brain (30 μ m) were stained with thionin. Sections containing the tip of the electrode tract were examined by two observers and plotted on coronal sections redrawn from the atlas of E. Fikova and J. Marsala [in *Electrophysiological Methods in Biological Research*, J. Bures, M. Petran, J. Achar, Eds. (Academic Press, New York, 1967), p. 653].
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Assortative Mating by Unwed Biological Parents of Adopted Children

Abstract. Analyses of data obtained from 662 unwed couples whose children were relinquished for adoption reveal that biological parents of adopted children mate assortatively. For physical characters, assortative mating of unwed parents was similar to that of wed parents; for behavioral characters, however, there was less assortative mating by the unwed parents. Because assortative mating inflates estimates of genetic parameters in adoption studies, future studies should collect information on both biological parents.

Although adoption studies are crucial for the genetic analysis of complex human behaviors (1), effects of assortative mating (similarity between mates) on such studies have not usually been considered. Because data have not been reported for unwed fathers, estimates of the importance of genetic factors have been based on the correlation between unwed mothers and their adopted children. These estimates, however, may be inflated if unwed parents mate assortatively. For example, if the "true" heritability of a character in a population is .5 and assortative mating for the trait is .4, the correlation between unwed mothers and their adopted children will estimate a heritability of .70—a situation not implausible for a character such as intelligence (as estimated by IQ) (2).

Married couples mate assortatively for many physical and behavioral characters (3). We now report that unwed biological parents of adopted children also mate assortatively. We obtained mate correlations for behavioral and physical characters of 662 unwed couples whose children were relinquished for adoption

through a nonresidential adoption agency in western United States from 1951 to 1976. The unwed parents provided most of the information during an interview with a social worker at the adoption agency, although it was often necessary for them to take the forms home in order to obtain information about their parents (the biological grandparents of the adopted child). For 25 percent of the files, the unwed father was available to answer questions about himself; for the rest, the unwed mother supplied information about the father (4). Nearly all the unwed parents were Caucasian.

The unwed couples represented a broad range of the population (Table 1). The mate correlations (assortative mating coefficients) for unwed and wed parents [who had participated in the Hawaii Study of Cognition (5)] are listed in Table 2. For the physical characters, with the exception of age, assortative mating coefficients of unwed couples do not differ significantly from those of wed parents. These coefficients are also similar to those reviewed by Spuhler (3) for married couples. In his review, the weighted

Table 1. Means, standard deviations (S.D.), and sample sizes (N) for unwed mothers and fathers.

Variables	Unwed mothers			Unwed fathers		
	Mean	S.D.	N	Mean	S.D.	N
Age	21.1	4.4	660	23.9	5.9	659
Education	12.6	2.9	661	13.0	3.1	647
Father's education*	11.9	4.0	580	12.6	3.1	291
Mother's education*	12.0	2.5	595	12.6	4.6	298
High school grade average†	2.8	0.6	330	2.6	0.7	202
Occupational NORC rating (11)	67.3	9.6	440	63.1	11.3	475
Father's NORC rating*	63.9	11.5	601	64.2	11.8	405

*Refers to the biological grandparents of the adopted child.

†Grades were converted to a four-point system in which the highest grade was 4.