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THEORETICAL REVIEW

Biological Bases for the Integration of Appetitive and Consummatory Grooming Behaviors in the Cat: A Review

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TRULSON, M. E. *Biological bases for the integration of appetitive and consummatory grooming behaviors in the cat: A review.* PHARMAC. BIOCHEM. BEHAV. 4(3) 329–334, 1976. – Cats with pontile lesions, frontal neocortical lesions, and thyroidectomized cats display a dissociation of the appetitive and consummatory components of grooming behavior following tactile stimulation of the body surface, an abnormal behavior which waxes and wanes with the seasons of the year. Tryptophan hydroxylase activity and serotonin levels were significantly decreased in the superior colliculi (but not other brain regions) in cats with pontile lesions or frontal neocortical lesions, but not in thyroidectomized cats. Systemic administration of 5-hydroxytryptophan or monoamine oxidase inhibition plus tryptophan administration abolishes the abnormal grooming behavior in each group of cats, and microinjections of 5-hydroxytryptophan or serotonin into the superior colliculi has the same effect, indicating that the change in a serotonergic system is a critical aspect of the abnormal behavior in cats with lesions and that a serotonergic system may also be involved in the genesis of the abnormal grooming behavior in thyroidectomized cats. Functional inactivation of the serotonergic system by *p*-chlorophenylalanine, LSD, or serotonin receptor blockade does not induce the abnormal grooming behavior in normal cats, indicating that other factors are involved. Cats with lesions and thyroidectomized cats display a rhythmic dysfunction in the excretion of glucocorticoids, and glucocorticoid administration abolishes the abnormal grooming behavior, suggesting that glucocorticoids are the other critical factor. Adrenalectomized cats do not display the abnormal grooming behavior, but when adrenalectomized cats are treated with *p*-chlorophenylalanine, the abnormal behavior appears. Thus, a serotonergic system in the superior colliculi, operating at some level of glucocorticoid function, is involved in the integration of appetitive and consummatory grooming behaviors.

Grooming behavior   Serotonin   Superior colliculus   Glucocorticoids   Thyroidectomy   CNS lesions

ALL major systems of behavior consist of complex components which are an integration of appetitive (learned) and consummatory (unlearned) behaviors put together into the adult, functional form. The concepts of appetitive and consummatory behaviors were developed by Sherrington [42] and elaborated by Craig [14]. Appetitive behavior is characterized by restless, varied forms of activity which serve to orient the animal toward the goal object. The consummatory action is an innate response which exhibits species-specific constancy. The genetically fixed, consummatory components of behavior appear first in ontongeny and with superimposed maturational and learning processes, emerge into the adult form [14]. The European ethologists (e.g., Lorenz & Tinbergen [26]) have emphasized the importance of the appetitive-consummatory behavioral dichotomy.

The physiological mechanisms underlying the integration of the appetitive and consummatory components of behavior is an issue of great theoretical importance, since knowledge of these mechanisms would provide valuable information concerning brain function. In studying the integration of appetitive and consummatory behaviors, the two components must first be separated, after which the physiological bases for their integration can be investigated. This type of investigation is possible in the case of grooming behavior, because there are ways to separate consummatory from appetitive components of the behavioral sequence. The present paper reviews studies on the anatomical and biochemical bases for the integration of appetitive and consummatory grooming behaviors in the cat.

The cat (*Felis catus* L.) displays three types of consummatory grooming responses: bites, licks, and scratches. The scratch is used to groom the head, neck, and shoulders and the bite and lick are used to groom the posterior portion of the body and the extremities. In the normal adult cat the appropriate consummatory response occurs after the tongue, teeth, or claws have been guided to the proper site on the body surface by the appetitive components of grooming behavior. That is, the appetitive and consummatory components of grooming behavior normally occur in a well integrated sequence, which is required to achieve the goal of maintaining a clean body surface.

Dogs and cats with frontal neocortical lesions were reported to display biting, licking and scratching movements when their body surfaces were tactually stimulated, as first described by Goltz, [21] in a dog, and later by Schaltenbrand and Cobb [39], Bard and Rioch [6] and Bradford [10] for cats. Randall [32] observed that cats with pontile lesions also displayed these elicitable biting, licking, and scratching movements, and we therefore undertook a systematic investigation of this behavioral phenomenon. Careful examination of these abnormal behaviors in cats with bilateral frontal neocortical lesions (which included all of the neocortex rostral to the ansate and anterior ectosylvian sulcus and dorsal to the rhinal fissure) and in cats with bilateral pontile lesions (which destroyed portions of the paralemniscal and central tegmental fields, pontile nuclei, middle cerebellar peduncle, and medial and lateral lemnisci) revealed that the elicitable movements were nondirected consummatory grooming bites, licks, and scratches.

Tactile stimulation of the body surface of a cat with a frontal neocortical or pontile lesion elicits a consummatory grooming bite, lick or scratch which appears immediately after stimulation and is not directed to the body surface. The type of response elicited is a response normally used to groom the region of the body surface that is tactually stimulated, and the best stimulus is one that simulates the normal consummatory grooming response. For example, scratching the cat on the neck or shoulders may elicit scratching movements of the hind leg, tapping the midline dorsal caudal area may elicit a consummatory grooming bite, and gently moving a finger along the body surface may elicit a consummatory grooming lick. But none of these consummatory grooming responses are directed to the body surface. Since the consummatory response occurs without the appetitive or orienting behavior that normally precedes it, the behavior is nonfunctional.

The classification of the elicitable movements as grooming behavior is based mainly on topographical criteria. For example, the elicited bite is a shallow scratching bite with the incisors and the canines and has the same frequency as the bite that is used by normal cats to groom. The premolars and molars are used in eating. The other kinds of bites, the prey-carrying bite, the kitten-carrying bite, the killing bite, the sex bite, all differ in frequency from the grooming bite and are not shallow bites confined to the surface. Not only is the elicited bite a grooming behavior, but the other elicitable behaviors (licking and scratching) also match the topography of normal consummatory grooming behaviors, and the type of response elicited is a response that is normally used to groom the region of the body surface that is tactually stimulated. Furthermore, although the initial elicited consummatory responses occur in midair, i.e., completely without an orienting component, when the stimulation continues for many seconds the cat may direct the consummatory response to his body surface and begin functional grooming.

Thus, the identification of consummatory grooming fragments is based on 4 criteria: (1) the topography of the responses matches that of the normal grooming repertoire; (2) the response appears immediately after tactile stimulation of the body surface and terminates immediately after the stimulation is discontinued; (3) the responses are not directed to the body surface but rather occur in midair; and (4) the response can be repeatedly elicited by tactile stimulation of a given area of the body surface. The locus and size of the responsive area shows considerable variation. In the studies reviewed below, a quantitative measure of the responsive area was obtained using standard diagrams of the right and left lateral views of a cat containing a grid pattern of dots (see [50] for illustration). Imitation bites (tapping the body surfaces), licks (gently moving a finger along the body surface), and scratches (actually scratching the body surface), were systematically directed to the cat's entire body surface, and the areas from which each type of consummatory grooming fragment could be elicited were entered on the diagram. The percentage of the body surface from which consummatory grooming fragments could be elicited was calculated by computing the fraction of the total number of dots enclosed within the responsive area.

Longitudinal monitoring of the behavioral abnormality in cats with lesions revealed that the size of the responsive area varies with the seasons of the year. The abnormality is most pronounced during the fall of the year, and an abnormal behavioral trough occurs during the summer [38]. The degree of the abnormality is at an intermediate level during the winter and spring. These variations occur in cats with lesions that are individually caged in a room kept at constant temperature, but with the lighting schedule synchronized with external lighting. Thus, the fluctuations in the abnormal grooming behavior may be related to changes in photoperiod or total luminous flux.

Histological signs of thyroid dysfunction (i.e., hyperplasia and colloid reduction in thyroid glands) were observed in cats with pontile lesions [32], and the rhythmical fluctuations in the size of the responsive area were found to coincide with fluctuations in thyroid activity [33]. This evidence suggested that thyroid hormones may be a critical factor for the lesion induced behavioral abnormality. Therefore, we thyroidectomized a group of normal cats and found that the same type of abnormal grooming behavior observed in cats with lesions also occurs in thyroidectomized cats, and that the size of the responsive area waxed and waned with the seasons of the year as in cats with lesions [36]. Subsequent studies, however, provided evidence that thyroid dysfunction is not a factor in the development of the abnormal behavior in cats with lesions. Thyroid hormone administration, which abolishes the abnormal grooming behavior in thyroidectomized cats, does not affect the abnormal behavior in cats with lesions, and thyroid hormone levels (thyroxine and triiodothyronine) in the brain and plasma of cats with lesions are not changed [36]. In a second longitudinal study of the correlation between the size of the responsive area and thyroid activity, thyroid function and seasonal variations in the abnormal behavior were not correlated [37]. The lesions apparently produce changes in certain measures of thyroid function, but these changes are incidental and not related to the modification of grooming behavior. The fact that thyroidectomized cats display the same abnormal behavioral rhythm as cats with lesions supports the conclusion that thyroid activity and size of responsive area are not related. Thus, thyroid hormones are not involved in the mechanism producing grooming fragments in cats with lesions, and the mechanism by which thyroidectomy and

TABLE 1

SUMMARY OF PHARMACOLOGICAL STUDIES ON THE ABNORMAL GROOMING BEHAVIOR*

Group	5HTP	MAOI plus Tryptophan	Tryptophan	PCPA	DOPA	Glucocorticoids
Normal	—	—	—	o[51]	—	—
Pontile Lesion	↓[51]	↓[47]	o[51]	↑[51]	o[35]	↓[36]
Frontal Neorcortical Lesion	↓[47]	↓[47]	o[47]	↑[47]	o[46]	↓[48]
Thyroidectomy	↓[46]	↓[47]	o[46]	↑[46]	o[46]	↓[36]
Adrenalectomy	—	—	—	↑‡	—	—
Adrenalectomy plus PCPA	↓‡	—	—	—	—	↓‡

*o, no effect on the degree of the grooming abnormality; ↑ , increases the degree of the grooming abnormality; ↓ , decreases the degree of the grooming abnormality; —, not tested. The superscript numbers indicate the reference for each study, and ‡ refers to data presented in this report.

lesions of the central nervous system (CNS) induce the same abnormal grooming behavior remained to be elucidated.

We then began a series of pharmacological studies designed to provide information concerning possible biochemical changes involved in the genesis of the abnormal grooming behavior. The results of these studies are summarized in Table 1. Systemic administration of 5-hydroxytryptophan (5HTP), which increases the levels of the neurotransmitter serotonin (5-hydroxytryptamine) in the brain [28], temporarily abolished the abnormal grooming behavior in cats with lesions and in thyroidectomized cats [46, 47, 51], while systemic administration of dihydroxyphenylalanine (DOPA), which increases cerebral catecholamine levels [28], had no effect on the abnormal behavior [35,46]. 5HTP abolishes the abnormal grooming behavior at a dose which produces no other dramatic behavioral changes. Pharmacological inhibition of central L-aromatic amino acid decarboxylase, which converts 5HTP to serotonin, blocked the effectiveness of 5HTP in abolishing the abnormal grooming behavior, indicating that 5HTP must be converted to serotonin to have its behavioral effect [35]. Administration of tryptophan, the initial precursor in serotonin biosynthesis, had no effect on the abnormal grooming behavior [46, 47, 51]. This is attributable to the fact that the activity of the enzyme tryptophan hydroxylase, which converts tryptophan to 5HTP, is rate limiting in the synthesis of serotonin [27], and administration of even very high doses of tryptophan produces only small increases in serotonin levels [29]. When tryptophan is administered in combination with a monoamine oxidase (MAO) inhibitor, (e.g., tranylcypromine or pargyline) thus blocking the catabolism of serotonin as well as increasing precursor levels, the concentration of serotonin within serotonergic neurons is substantially increased [1,22]. This treatment abolishes the abnormal grooming behavior in cats with pontile or frontal neocortical lesions and in thyroidectomized cats [47]. Since MAO inhibitors do not increase catecholamine levels in cats [17, 41, 43], this is evidence for a specific involvement of serotonin. Administration of a tryptophan hydroxylase inhibitor, *p*-chlorophenylalanine [PCPA], to deplete serotonin [25, 49, 55] in cats with lesions or in thyroidectomized cats displaying few or no grooming fragments (because of spontaneous seasonal reversions, discussed above) increases the degree of the behavioral abnormality [46, 47, 51]. Thus, serotonin was implicated in the mediation of the abnormal grooming behavior.

Virtually all serotonin in the CNS is contained within the cell bodies of the brainstem raphe complex and their axon processes, which innervate all levels of the neuraxis [15, 20, 53]. The next important question was the locus in the CNS where serotonin exerted its effect of abolishing grooming fragments. Since the abnormal grooming behavior occurs only after tactile stimulation of the body surface, we ablated brain regions known to receive somesthetic input. When the superior colliculi were ablated in cats with lesions or thyroidectomy, the abnormal grooming behavior could no longer be elicited [46,51]. We then began a series of studies involving microinjections of substances directly into various brain regions through chronically implanted cannulae in freely moving cats. Microinjections of 5HTP or serotonin (but not gamma-amino-butyric acid, norepinephrine, tryptophan or vehicle) into the superior colliculi (but not other brain regions) abolished the abnormal grooming behavior in cats with lesions or thyroidectomy [46,51]. These data suggested that there was a defect in serotonin metabolism in the superior colliculi of cats that displayed the abnormal grooming behavior. Neurochemical studies revealed that tryptophan hydroxylase activity and serotonin levels were significantly decreased in the superior colliculi (but not in the hypothalamus, dorsal thalamus, cerebral neocortex or cerebellum) in cats with lesions, but no changes were found in thyroidectomized cats [47,50].

The decrease in tryptophan hydroxylase activity and serotonin levels in the superior colliculi after pontile or frontal neocortical lesions cannot be explained in terms of the interruption of direct projections of serotonergic neurons, since there are no serotonergic cell bodies or fibers of passage in the regions of the lesions [31]. This indicates that the changes are mediated transneuronally. The serotonergic system that projects to the superior colliculi may receive a facilitatory input from the frontal neocortical and pontile regions, and lesioning these areas would decrease the activity of these neurons. Both the frontal neocortical and pontile lesions interrupt fibers to the raphe nuclei [11,40], as well as to the superior colliculi [3,44]. Several studies have reported a positive correlation between nerve impulse flow and neurotransmitter synthesis. For example, LSD, which decreases the discharge rate of serotonergic neurons by acting directly on the cell body [2], or section of monoamine fiber systems leads to a decrease in serotonin synthesis and turnover [13,19]. Since the pontile and frontal neocortical lesions do not directly interrupt serotonergic neurons, the change in serotonin metabolism seen in the superior colliculus may be a secondary change due to a decrease in nerve impulse flow.

The fact that either 5HTP or MAO inhibition plus tryptophan administration abolishes the abnormal grooming behavior in thyroidectomized cats suggests that thyroid hormones may affect serotonergic neurons. However, neither tryptophan hydroxylase activity nor serotonin levels were significantly decreased in thyroidectomized cats [47]. Recent studies have indicated that thyroid hormones affect the sensitivity of monoamine receptors in the CNS [16,23], and the defect in the serotonergic system following thyroidectomy may be a decrease in receptor sensitivity.

If a decrease in the availability of serotonin at receptors is the only critical change required to induce the abnormal grooming behavior, then pharmacological manipulations which produce this defect should induce the abnormal grooming behavior in normal cats. However, neither systemic nor local (superior colliculi) injections of PCPA induced the abnormal grooming behavior in normal cats [50,51]. Similarly, administration of serotonin receptor blocking agents (Cinnaserin or methysergide) or LSD, which also inactivate the brain raphe-serotonin system [2,49], did not produce the abnormal behavior in any of the normal cats tested [47]. Therefore, it appeared that pontile lesions, frontal neocortical lesions and thyroidectomy produced some other change that was critical for inducing the abnormal grooming behavior.

Because the activity of the endocrine system shows prominent seasonal variations, the seasonal variations in the degree of the behavioral abnormality suggested that some endocrine factor may be involved. Investigation of this question revealed a rhythmical dysfunction in the urinary excretion of 11-hydroxycorticoids, which was inversely correlated with the size of the responsive area in cats with lesions and in thyroidectomized cats [34,36]. That is, glucocorticoid excretion was low when the behavioral abnormality was most prominent. If the glucocorticoid defect was a critical feature of the abnormal grooming behavior, then glucocorticoid administration would be expected to change the abnormal behavior. Systemic administration of glucocorticoids abolished the abnormal grooming behavior in cats with lesions and in thyroidectomized cats [36,48]. Furthermore, microinjections of glucocorticoids into the superior colliculi also abolished grooming fragments [48]. The abnormal grooming behavior could not be induced by adrenalectomy [34,47], indicating that the behavioral abnormality is not related solely to glucocorticoid activity. This suggested that, even though there are interrelationships between serotonin metabolism and glucocorticoids [4, 5, 30], the lesions and thyroidectomy produce two independent defects which induce the abnormal grooming behavior.

To test the hypothesis that the lesions and thyroidectomy produce 2 independent defects, the following experiment was performed. A group of normal, adult male cats received bilateral adrenalectomies according to the method of Hopcroft [24] and were maintained on a saline drinking solution, while an additional group of normal cats received sham surgery. Two weeks after surgery each cat received daily injections of PCPA (methyl ester HCl, 150 mg/kg/day, IP). The abnormal grooming behavior appeared in each of the adrenalectomized cats after 3 to 5 consecutive days of PCPA administration, while none of the sham operated controls receiving PCPA displayed any of the abnormal behavior. The abnormal grooming behavior in PCPA-treated adrenalectomized cats could be abolished by systemic administration of either 5HTP (25 mg/kg, IM) or glucocorticoids (30 mg/kg/day for 3 consecutive days, IM) (Trulson, unpublished data). These data indicate that critical deficits in both serotonin and glucocorticoids are required to produce the abnormal grooming behavior. Because adrenalectomy or serotonin depletion alone do not induce the abnormal grooming behavior, pontile lesions, frontal neocortical lesions and thyroidectomy apparently produce 2 deficits independently, i.e., the serotonin defect is not a sequela of the glucocorticoid defect, and vice versa.

Variations in levels of serotonin may be responsible for the seasonal variation in the abnormal behavior. Seasonal variations in serotonin have not been investigated in the cat, but an annual rhythm in cerebral serotonin levels has been found in the rat [54]. The seasonal variations in the abnormal grooming behavior are probably not mediated by serotonergic neurons indirectly via an effect on glucocorticoids [30] because PCPA induces the abnormal grooming behavior in adrenalectomized cats, and the abnormal behavior may then be attenuated by administering 5HTP. Thus even though serotonergic neurons may regulate adrenalcortical function, the PCPA effect of inducing the abnormal behavior is independent of any direct action on the adrenal cortex but requires lowered levels of glucocorticoids as a requisite condition. Similar quantitative effects on the abnormal behavior have also been obtained with glucocorticoids: when the abnormal grooming behavior is induced in adrenalectomized cats with PCPA, the abnormal behavior can then be abolished by the administration of glucocorticoids. Thus the situation is complex and either rhythmic variations in serotonin or glucocorticoids (or the rhythmic interactions of the 2) may account for the spontaneous reversions of the abnormal grooming behavior. It is clear (1) that decreased serotonin and glucocorticoids are essential and sufficient conditions for inducing the abnormal grooming behavior, and (2) that either exogenous 5HTP or exogenous glucocorticoids is sufficient to abolish the abnormal grooming behavior.

Grooming is an important adaptive behavior, the essential function of which is to maintain the integrity of a surface that separates two radically different environments. Many diverse and complex behavioral repertoires are involved in grooming behavior so that "care of the body surface behavior" is listed as a "major instinct" by Tinbergen [45] and Fletcher [18], together with such behaviors as eating, drinking, reproductive behavior and sleep. The survival value of grooming (as well as eating, drinking, etc.) concerns homeostasis [12]. While eating and drinking make direct contributions to the internal milieu, grooming has the critical and unique function of maintaining the requisite boundary for the homeostated system. A large amount of time is spent in grooming the body surface. Grooming behavior occupies 40% of the awake time of rats [9] and 67% of the nonsleeping, nonresting time of cats [52]. Any procedure which decreases the efficiency of grooming (e.g., toe amputations or limb paralysis) has immediate deleterious effects and may cause the death of the animal [7,8]. Time lapse film analysis of spontaneous grooming behavior in cats with pontile lesions, frontal neocortical lesions, and thyroidectomized cats revealed that each group of cats spent less of their total time grooming and were less efficient in grooming than normal cats [52]. In some of these cats the fur becomes thick and matted, and skin lesions develop. The superior colliculus is not essential for the integration of appetitive and consummatory grooming behaviors because cats with superior colliculi lesions display spontaneous grooming behavior. However, cats with lesions of the superior colliculi also spend less of their total time grooming and are less efficient in grooming than normal cats.

The classical view of the functions of the superior colliculus is in terms of correlation and sensation. The studies reviewed here indicate that a serotonergic system in the superior colliculus, operating at some level of glucocorticoid function, is involved in relating somesthetic sensation to the integration of appetitive and consummatory grooming behaviors. Perhaps some of the correlation and sensation mediated by the superior colliculus and its prominent serotonergic input involves the correlation of appetitive and consummatory grooming behaviors until the sensation of a clean body surface is obtained.

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REFERENCES

1. Aghajanian, G. K., and I.M. Asher. Histochemical fluorescence of raphe neurons; selective enhancement by tryptophan. *Science* **172:** 1159–1161, 1971.
2. Aghajanian, G. K., H. H. Haigler and F. E. Bloom. Lysergic acid diethylamide and serotonin: direct actions on serotonin-containing neurons in rat brain. *Life Sci.* **11:** 615–622, 1972.
3. Altman, J. and M. B. Carpenter. Fiber projections of the superior colliculus in the cat. *J. comp. Neurol.* **116:** 157–177, 1961.
4. Azmitia, E., S. Algeri and E. Costa. *In vivo* conversion of ^{3}H-L-tryptophan into ^{3}H-serotonin in brain areas of adrenalectomized rats. *Science* **169:** 201–203, 1970.
5. Azmitia, E. and B. S. McEwen. Corticosterone regulation of tryptophan hydroxylase in midbrain of the rat. *Science* **166:** 1274–1276, 1969.
6. Bard, P. and D. Rioch. A study of four cats deprived of neocortex and additional portions of the forebrain. *Johns Hopkins Hosp. Bull.* **60:** 73–147, 1937.
7. Bell, J. G., C. M. Clifford, G. J. Moore and G. Raymond. Effects of limb disability on lousiness in mice. III. Gross aspects of acquired resistance. *Exp. Parasit.* **18:** 49–60, 1966.
8. Bell, J. G., W. L. Jellison and C. R. Owen. Effects of limb disability on lousiness in mice. I. Preliminary studies. *Exp. Parasit.* **12:** 176–183, 1962.
9. Bolles, R. Grooming behavior in the rat. *J. comp. physiol. Psychol.* **53:** 306–310, 1960.
10. Bradford, F. Ablations of frontal cortex in cats with special reference to enhancement of the scratch reflex. *J. Neurophysiol.* **2:** 192–201, 1939.
11. Brodal, A., F. Walberg and E. Taber. The raphe nuclei of the brain stem in the cat. III. Afferent connections. *J. comp. Neurol.* **114:** 261–279, 1960.
12. Cannon, W. *The wisdom of the body.* New York: W. W. Norton, 1932.
13. Carlsson, A., P. Bedard, M. Lindqvist and T. Magnusson. Influence of nerve-impulse flow on the synthesis and metabolism of 5-hydroxytryptamine in the central nervous system. *Biochem. Soc. Symp.* **36:** 17–32, 1972.
14. Craig, W. Appetites and aversions as constituents of instincts. *Biol. Bull.* **34:** 91–107, 1918.
15. Dahlstrom, A. and K. Fuxe. Evidence for the existence of monoamine neurons in the central nervous system. II. Experimentally induced changes in the intraneuronal amine levels of bulbospinal neuron system. *Acta physiol. scand. Suppl. 247:* **64:** 1–36, 1965.
16. Engstrom, G. T., H. Svensson and B. Waldeck. Thyroxine and brain catecholamines: increased transmitter synthesis and increased receptor sensitivity. *Brain Res.* **77:** 471–483, 1974.
17. Feldberg, W. and V. J. Lotti. Body temperature responses in cats and rabbits to the monoamine oxidase inhibitor tranylcypromine. *J. Physiol.* **190:** 203–220, 1967.
18. Fletcher, R. *Instinct in man.* New York: Shocken, 1966.
19. Freedman, D. X. and W. O. Boggan. Brain serotonin metabolism after tolerance dosages of LSD. In: *Adv. Biochem Psychopharm,* edited by E. Costa, G. L. Gessa and M. Sandler. **10:** 151–157, 1974.
20. Fuxe, K. Evidence for the existence of monoamine neurons in the central nervous system. IV. The distribution of monoamine terminals in the central nervous system. *Acta physiol. Scand. Suppl. 247:* **64:** 41–85, 1965.
21. Goltz, F. Der Hund ohne Grosshirn. *Pfleugers Arch. ges. Physiol.* **51:** 570–614, 1892.
22. Grahame-Smith, D. G. Studies *in vivo* on the relationship between brain tryptophan, brain 5HT synthesis and hyperactivity in rats treated with a monoamine oxidase inhibitor and L-tryptophan. *J. Neurochem.* **18:** 1053–1066, 1971.
23. Green, A. R. and D. G. Grahame-Smith. TRH potentiates behavioral changes following increased brain 5-hydroxytryptamine accumulation in rats. *Nature* **251:** 524–526, 1974.
24. Hopcroft, S. A technique for the simultaneous bilateral removal of the adrenal glands in guinea pigs, using a new type of safe anesthetic. *Expl Med. Surg.* **24:** 12–19, 1966.
25. Koe, B. and A. Weissman. *p*-Chlorophenylalanine: A specific depletor of brain serotonin. *J. Pharmac. exp. Ther.* **154:** 499–516, 1966.
26. Lorenz, K. and N. Tinbergen. The comparative method of studying innate behavior patterns. *Physiological mechanisms in animal behavior.* Cambridge University Press, 1950.
27. Lovenberg, W., E. Jequier and A. Sjoerdsma. Tryptophan hydroxylation: measurement in pineal gland, brain stem, and carcinoid tumor. *Science* **155:** 217–219, 1967.
28. McGeer, P. L., E. G. McGeer and J. A. Wada. Central aromatic amine levels and behavior. *Archs Neurol.* **9:** 91–99, 1963.
29. Moir, A. T. B. and D. Eccleston. The effects of precursor loading in the cerebral metabolism of 5-hydroxyindoles. *J. Neurochem.* **15:** 1093–1101, 1968.
30. Naumenko, E. V. *Central regulation of the pituitary-adrenal complex.* New York: Consultants Bureau, 1973, pp. 97–139.
31. Pin, C., B. Jones and M. Jouvet. Topographie des neurons monoaminergiques du tronc du chat: etude par histofluorescence. *C. r. Séanc. Soc. Biol.* **162:** 2136–2141, 1968.
32. Randall, W. The behavior of cats (*Felis catus* L.) with lesions in the caudal midbrain region. *Behavior* **23:** 107–139, 1964.
33. Randall, W. and J. Liittschwager. The relationship between cyclic changes in thyroid function and behavior of cats with brain stem lesions. *J. psychiat. Res.* **5:** 39–58, 1967.

34. Randall, W. and V. Parsons. Rhythmic dysfunctions in 11-hydroxycorticoid excretion after midbrain lesions and their relationship to an abnormal grooming behavior in cats. *J. Interdiscip. Cycle Res.* **3:** 3–24, 1972.
35. Randall, W. and M. Trulson. A serotonergic system involved in the grooming behavior of cats with pontile lesions. *Pharmac. Biochem. Behav.* **2:** 355–360, 1974.
36. Randall, W., M. Trulson and V. Parsons. Role of thyroid hormones in an abnormal grooming behavior in thyroidectomized cats and cats with pontile lesions. *J. comp. physiol. Psychol.* **90:** 231–243, 1976.
37. Rogers, W. R. Rhythmic variations during a year in grooming behavior, thyroid activity, and body weight of normal and midbrain lesioned cats. Unpublished Master's Thesis, The University of Iowa, 1970.
38. Rogers, W., V. Parsons and W. Randall. Consummatory grooming fragments: a model for periodic behavior. *Psychon. Sci.* **23:** 375–376, 1971.
39. Schaltenbrand, G. and S. Cobb. Clinical and anatomical studies on two cats without neocortex. *Brain* **53:** 449–488, 1930.
40. Scheibel, M. E. and A. B. Scheibel. Structural substrates for integrative patterns in the brain stem reticular core. In: *Reticular Formation of the Brain.* Boston: Little, Brown and Co., 1958, pp. 31–55.
41. Schoepke, H. G. and R. G. Wiegand. Relation between norepinephrine accumulation or depletion and blood pressure responses in the cat and rat following pargyline administration. *Ann. N. Y. Acad. Sci.* **107:** 924–934, 1963.
42. Sherrington, C. *The integrative action of the nervous system.* New Haven: Yale University Press, 1906, pp. 325 ff.
43. Spector, S. Monoamine oxidase in control of brain serotonin and norepinephrine content. *Ann. N. Y. Acad Sci.* **107:** 856–864, 1963.
44. Sprague, J. Cortico-fugal projections to the superior colliculus in the cat. *Anat. Rec.* **145:** 288, 1963.
45. Tinbergen, N. *The study of instinct.* London: Oxford University Press, 1951.
46. Trulson, M. E. Relationship of a serotonergic system in the superior colliculus and glucocorticoids to elicitable consummatory grooming fragments in cats with pontile lesions, frontal neocortical lesions, and in thyroidectomized cats. Doctoral Dissertation, The University of Iowa, 1974.
47. Trulson, M. E. Role of superior colliculus serotonin in the grooming behavior of cats. *Neuropharmacology* **15:** 91–97, 1976.
48. Trulson, M., J. Elbin and W. Randall. Role of glucocorticoids an abnormal grooming behavior in cats with pontile or frontal neocortical lesions. (Submitted for publication.)
49. Trulson, M. E. and B. L. Jacobs. LSD acts synergistically with serotonin depletion: Evidence from behavioral studies in cats. *Pharmac. Biochem. Behav.* (in press).
50. Trulson, M., J. Nicolay and W. Randall. Abnormalities in grooming behavior and tryptophan hydroxylase activity in the superior colliculi in cats with pontile and frontal neocortical lesions. *Pharmac. Biochem. Behav.* **3:** 87–94, 1975.
51. Trulson, M. and W. Randall. 5-hydroxytryptamine metabolism, superior colliculus and grooming behavior in cats with pontile lesions. *J. comp. physiol. Psychol.* **85:** 1–10, 1973.
52. Trulson, M., R. Swenson and W. Randall. Effects of frontal neocortical lesions, thyroidectomy, and adrenalectomy on grooming behavior in cats. (Submitted for publication.)
53. Ungerstedt, U. Stereotaxic mapping of the monoamine pathways in the rat brain. *Acta physiol. scand. Suppl.* **367:** 1–48, 1971.
54. Valzelli, L. and S. Garattini. Behavioral changes and 5-hydroxytryptamine turnover in animals. *Adv. Pharmac.* **6:** 249–260, 1968.
55. Zitrin, A., F. Beach, J. Barchas and W. Dement. Sexual behavior of male cats after administration of parachlorophenylalanine. *Science* **170:** 868–870, 1970.