reveal any significant homologies between these cryptic peptides and peptides of known structure (*29*). Alternatively, these peptides may serve structural roles, important for the proper folding of the precursor into a conformation that allows its accurate proteolytic processing by tissue-specific proteases during the formation of calcitonin, or they may serve simply as inert protein spacers without specific biological activities. These cellular cleavages of the calcitonin precursor may differ in different tissues, such as the thyroid and brain, comparable with the processing of the common precursor of ACTH, MSH, and the endorphins (*30*), in which the cleavage in the anterior and in the intermediate lobe of the pituitary is different. The knowledge that the precursor is glycosylated (*29*) and contains peptide sequences attached to calcitonin raises the possibility that forms of the hormone detected in the circulation, with apparent molecular weights larger than calcitonin, may result from incomplete processing of the precursor prior to secretion in vivo (*31*). The chemical synthesis of the peptide extensions of the calcitonin precursor should be useful for several purposes, including the preparation of radioimmunoassays that can be used for the detection of the precursor-specific peptides during intracellular processing and for analyses of the immunochemical composition of the multiple circulating forms of calcitonin.

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Species-Typical Behavior of Hamsters Deprived from Birth of the Neocortex

Abstract. *Hamsters deprived from birth of the neocortex developed normally and displayed the usual hamster-typical behavioral patterns. With the additional concurrent destruction of midline limbic convolutions (cingulate and underlying dorsal hippocampal), there were deficits in maternal behavior and a lack of development of play behavior. These findings demonstrate in a rodent (i) that the striatal complex and limbic system, along with the remaining neuraxis, are sufficient for giving expression to a wide range of unlearned forms of species-typical behavior and (ii) that midline limbic structures are required for the expression of play behavior and the integrated performance of maternal behavior.*

The purpose of this study was to test the hypothesis that in rodents the two older evolutionary formations of the forebrain [the striatal complex and the limbic system (*1, 2*)] are sufficient, along with the remaining nervous system, for the expression of most forms of species-typical behavior. Respective parts of the mammalian striatal complex and limbic system reflect an ancestral relationship to reptiles and early mammals (*3*). We found that hamsters deprived from birth of the neocortex grew normally and displayed the usual hamster-typical behavioral patterns seen under laboratory conditions (*4*). The findings are at variance with the popular view that in mammals generally the neocortex is required for fully integrated, directed behavior.

The subjects were Syrian golden hamsters (*Mesocricetus auratus*) descended from wild hamsters captured in 1971 (*5*). The neocortex was eliminated by heat applied to the skull or by aspiration (under cryoanesthesia) on the first or second day after birth. Littermates used as controls received similar treatment, but without the destruction of brain tissue (Fig. 1A). After surgery the pups were returned to the dam. The day-to-day behavioral development was recorded on a checklist derived from an extensive ethogram (*6*). Time-lapse television was used for 24-hour observations of animals living in special habitats. Quantitative measures of mating and certain other behaviors were obtained by the use of a computer-assisted event recorder.

On the basis of the gross and microscopic examination of the brains in 13 animals, we describe (i) the behavior of hamsters deprived of the neocortex and (ii) the behavior of those with the additional loss of the midline limbic convolutions. Figure 1B shows the brain of a female hamster in which all of the neocortex except a remnant at the right frontal pole was absent. In correspondence with the absence of the neocortex, there was only a remnant of the corpus callosum, a great reduction of the neothalamus (including the "specific" somatosensory, visual, and auditory nuclei), a virtual disappearance of the pyramids, and a decrease in size of the neocerebellum.

Hamsters devoid of neocortex grew at the normal rate and resembled their littermates with respect to the time of development of hamster-typical behavior. The list of observed behaviors included thermotaxis, play-fighting, digging, seed cracking, food pouching, hoard and nest building, tunnel blocking, scent marking, aggression, territorial defense, circadian activity rhythms, species preference, mating, and breeding.

When presented a choice between a member of their own or another species of hamster (*M. brandti*), experimental animals of both sexes showed a strong sexual preference for their own species. Although males without neocortex had some motor difficulty during mating and required twice the usual number of intromissions to achieve ejaculation, they displayed normal sexual arousal, performed the complete copulatory act, and successfully impregnated females. Experimental females showed an estrous cycle, readily copulated with males, conceived, gave birth, and successfully reared their young. The female whose brain is shown

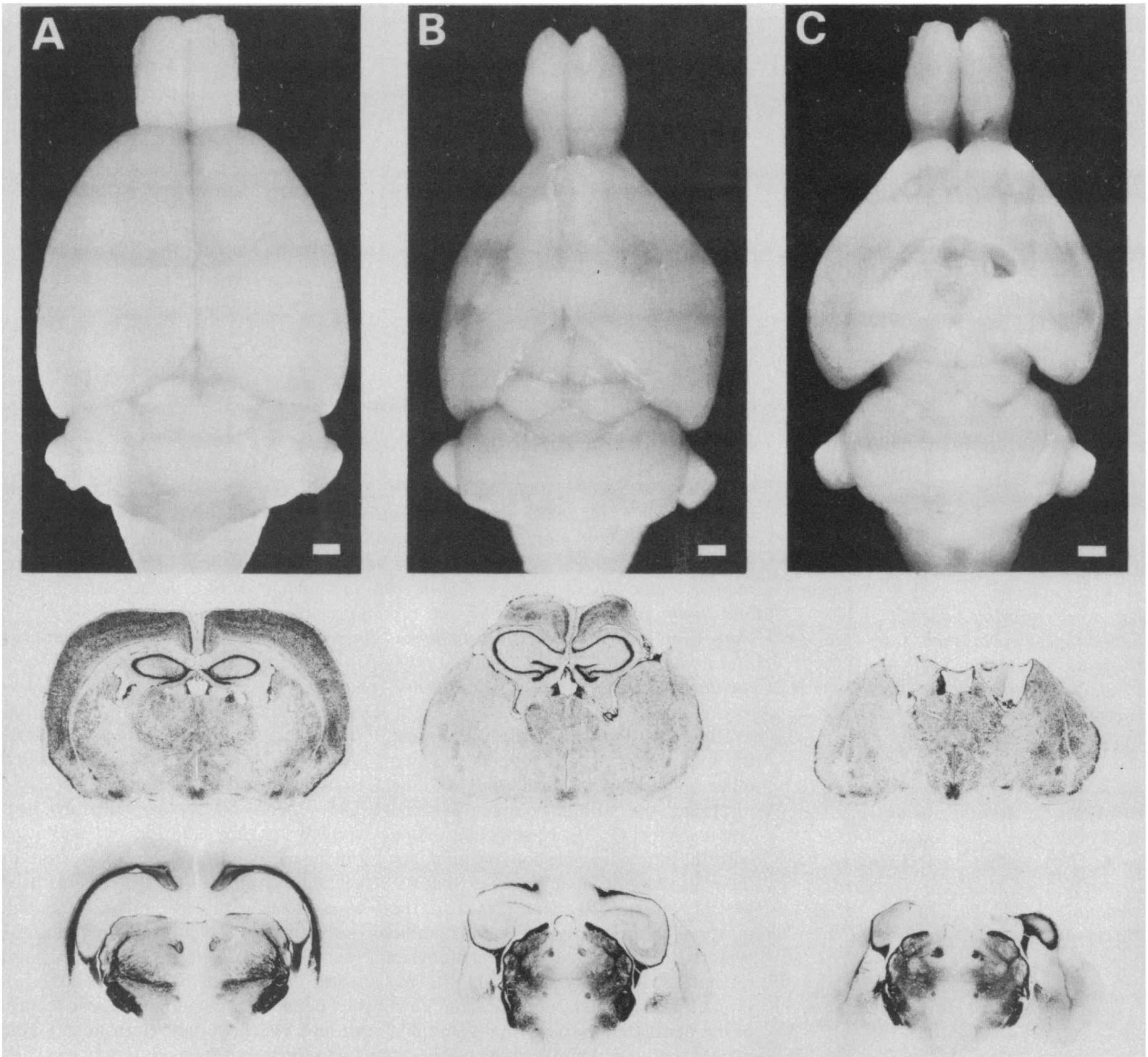

Fig. 1. Dorsal view of brains of a control (A) and two experimental hamsters (B and C), with representative coronal sections through the diencephalon. (B) Brain of a female without the neocortex except for a remnant at the right frontal pole. The cortex seen above the hippocampus is limbic cortex of the cingulate area. The fibrous molecular layer helps to identify the lateral limits of the cingulate cortex in rodents. (C) Female brain with the additional loss of midline limbic convolutions (cingulate gyrus and underlying hippocampus). The first row of sections, stained for cells, shows a similar plane through the anterior thalamus. A plane through the posterior thalamus is shown in the fiber-stained sections in row 2. Note the great reduction of neothalamic structures in sections from (B) and (C). The white bars correspond to 1 mm.

in Fig. 1B gave birth to a litter of five pups and, although somewhat clumsy in retrieval, reared all of them.

Four hamsters in which there was an additional loss of the midline limbic structures (cingulate convolution and the underlying dorsal part of the hippocampus) (Fig. 1C) retained most of the listed hamster-typical forms of behavior, with the notable exceptions that they displayed no play-fighting during development and exhibited severe deficits in maternal behavior. The female whose brain is shown in Fig. 1C gave birth to a litter of eight pups and nursed them, but failed completely in pup retrieval. Like the other female in this category, she performed an excessive number of scent marks and sexually presented to a male separated by a screen. The animals without neocortex were generally more difficult to handle than the controls; but those with additional loss of the midline limbic structures exhibited a ferocity that led their handlers to refer to them as "wild." In addition, they engaged in stereotyped pacing suggestive of caged animals in a zoo; video analysis revealed that an average of 6.5 hours per day was spent in such activity as opposed to 0.5 hours for controls.

The deficits in play-fighting and parental care are of particular interest because two cardinal developments in the evolution from reptiles to mammals were the origination of nursing and maternal care of offspring and play behavior (*2*). The midline limbic cingulate cortex has been implicated in maternal behavior (*7*), but there has been no previous evidence that the limbic cortex of the medial wall of the hemisphere is involved in play.

In related investigations of brain mechanisms underlying species-typical communication, it was found that in animals as diverse as lizards and monkeys lesions of certain parts of the striatal complex interfere with social display behavior (*8*). Our present study adds new dimensions to these observations by demonstrating in a rodent that the striatal complex and limbic system, with the remaining neuraxis, are sufficient for giving expression to a wide range of unlearned forms of species-typical behavior and that the midline limbic structures are required for the expression of play behavior and integrated performance of maternal behavior.

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1. The mammalian striatal complex consists of the olfactostriatum (olfactory tubercle and nucleus accumbens), corpus striatum (caudate-putamen), globus pallidus, and satellite collections of gray matter (*2*). The limbic system includes the cortex of the limbic lobe and structures of the brainstem with which it has primary connections [P. D. MacLean, *Electroencephalogr. Clin. Neurophysiol. J.* **4**, 407 (1952)].
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Parasitism and Behavioral Dominance Among Male Mice

Abstract. *Infestations by the nematode* Heligmosomoides polygyrus *can prevent adult male mice from becoming behaviorally dominant. The effect is dose-dependent and is more likely to influence the development of dominance than to disrupt existing dominance relationships. Doses capable of exerting this effect are not lethal and do not affect weight.*

Hausfater and Watson (*1*) observed an inverse relation between dominance status in male baboons and fecal output of helminth eggs and protozoan cysts, but did not imply that parasitic infestation affects the development of dominance in males. I investigated whether and under what circumstances a helminth (*Heligmosomoides polygyrus*) can influence dominance relationships among male laboratory mice.

Table 1. Results of the first experiment.

Larvae administered	Groups	Groups in which uninfected mouse became dominant	χ^2	*P*
50	21	7	0.0536	>.05
150	30	15	3.0375	>.05
250	20	14	11.5931	<.005

Table 2. Results of the second experiment.

Larvae administered	Groups	Groups in which dominant mouse became subordinate	χ^2	*P*
0	19	3		
50	20	1	1.2323	>.05
150	21	1	1.3478	>.05
250	19	5	0.6333	>.05

Two experiments were carried out. The first was designed to determine whether various doses of the helminth could prevent the development of behavioral dominance among males that previously had not encountered one another. The second experiment was designed to determine whether equivalent doses of the helminth could disrupt established dominance relationships.

In the first experiment, 21-day-old male CF1 mice were housed individually and kept isolated for 5 weeks. They were then marked, weighed, and housed in groups of three. Two mice in each group received a dose of *H. polygyrus* (50, 150, or 250 larvae, orally) (*2*). After 14 days the dominance status of each mouse was determined (*3*), and it was killed and weighed. In the second experiment, 21-day-old male CF1 mice were housed individually and kept isolated for 3 weeks. Then they were marked and housed in groups of three. After 2 weeks the dominant mouse in each group was identified and inoculated (50, 150, or 250 larvae), and all the mice were weighed. After 2 weeks dominance status was again determined and the mice were killed and weighed. Nineteen groups of control mice were treated in the same