Evidence for Higher Functions of the Cerebellum: Eating and Grooming Elicited by Cerebellar Stimulation in Cats

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ABSTRACT Well-organized eating and grooming behaviors were elicited in cats by stimulation of a zone in the cerebellum that extended from the fastigial nucleus to the superior cerebellar peduncle. Behaviors appeared to result from the facilitation of specific sensorimotor mechanisms, rather than the induction of generalized "drive" states. The results emphasize the need for a broad view of cerebellar function.

Several studies have investigated the effects of electrical stimulation of localized areas of the cerebellum in unanesthetized free-moving cats (1-6). The predominant effects reported have been relatively simple autonomic or tonic motor responses, such as pressor responses or postural changes. A few papers, however, have reported somewhat more complex responses such as licking, biting, or swallowing movements (5, 6). Furthermore, in a previous study Bernston showed that coordinated sequences of grooming behavior can be elicited by stimulation of the superior cerebellar peduncle (7). In the present study, we examined the behavioral effects of electrical stimulation of the cerebellum in unanesthetized free-moving cats which were provided with a variety of goal objects, to determine whether grooming or other complex behaviors can be elicited from the cerebellum itself.

The subjects were 15 cats, each surgically implanted with 16 chronic monopolar stimulation electrodes aimed for different regions of the cerebellum. Anatomical data from three additional cats of a previous study (7) are also included. After at least 5 days of postoperative recovery, food- and water-satiated cats were given two free-moving cerebellar stimulation tests separated by at least 24 hr. During each of these tests, all electrodes were tested at a wide range of voltage levels, with 50-Hz monopolar pulses of 100-μsec duration. The testing box (73 x 54 x 48 cm) contained dry cat chow, an anesthetized rat, and a foam-rubber block and a wood block each of about the same dimensions as a rat. After completion of testing, the brains were perfused with formalin, sectioned, and stained. Electrodes were localized by direct projection of the sections onto atlas diagrams of Snider and Niemer (8).

Only those electrodes that produced consistent behaviors in both testing sessions are reported as effective. Details of the surgical, histological, and experimental procedures are essentially the same as those described in an earlier paper (7).

Cerebellar stimulation evoked two main categories of complex species-characteristic behavior, eating and grooming (Table 1), in addition to more elementary motor responses which have been described in detail (1-6). Generally, elicited eating and grooming were vigorous, reliable, and stimulation-bound. Without stimulation, eating and grooming were virtually never seen under the conditions of the tests.

Stimulation-induced eating resembled normal eating behavior. Upon stimulation, the cats approached the food, picked up pieces with their front teeth, shifted the food to the back of their mouths, and then chewed and swallowed it. The cats, however, did not appear to search out the food as actively as food-deprived cats, and would approach and eat the food only if it was visible and located nearby. Despite being fully satiated, the two cats showing the strongest stimulation-bound eating ate 150 and 97 g of food in a 1-hr test during which they were stimulated for 1 min out of each 3 min.

Stimulation also induced chewing and swallowing of non-nutritive objects, such as small pieces of bedding, cork, or rubber. In most cases, stimulation did not induce lapping of food that had been liquified in a blender. Furthermore, hungry cats which were lapping highly preferred liquified tuna before stimulation, promptly left it and began eating dry cat chow when stimulated. These findings suggest that cerebellar stimulation may have specifically facilitated the chewing and swallowing components of eating behavior rather than induced a more generalized "hunger drive."

Stimulation-induced grooming included fur licking and groom-biting. Groom-biting consisted of gnawing and pulling at the fur with the front teeth, as though the cat were trying to remove a burr. With continued stimulation, the orientation of elicited grooming generally shifted progressively from one region of the fur to another. The presence of foreign objects in the fur tended to increase the grooming directed toward that region, suggesting that elicited grooming was not a completely undirected motor automatism. Six cats were given a grooming orientation test with tape placed, in counterbalanced order, at one of two sites on the fur. The mean time spent grooming

Table 1. Number of electrodes yielding eating and grooming, mean thresholds, and number of electrodes yielding "pure" behaviors

<table>
<thead>
<tr>
<th></th>
<th>Grooming</th>
<th>Eating</th>
</tr>
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<tbody>
<tr>
<td>No. of effective electrodes</td>
<td>29</td>
<td>14</td>
</tr>
<tr>
<td>Mean threshold (volts)</td>
<td>4.3</td>
<td>4.9</td>
</tr>
<tr>
<td>No. of electrodes yielding pure responses*</td>
<td>17</td>
<td>2</td>
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* Unaccompanied by the other behavior.
the taped site during the twelve 30-sec trials for each cat was 12.7 sec, compared to 3.9 sec for the nontaped site (t = 4.19, df = 5, P < 0.01).

While elicited grooming was largely directed to the cat's own fur, most cats would also groom the fur of a nearby anesthetized rat. Nonfurry objects such as blocks of foam or wood were virtually never groomed, which suggests that sensory cues of fur may have been important in determining the orientation of elicited grooming. The finding that cats would groom a rat rules out the possibility that grooming was induced by, and directed to, a localized elicited sensation. Grooming of the face and head with the forepaws, a salient component of natural grooming, was never elicited in the present study, which suggests that stimulation may not have induced a generalized "grooming drive." Rather, the results seem more consistent with the view that cerebellar stimulation produced a strong facilitation of the specific sensorimotor mechanisms for the licking and groom-biting components of grooming.

We feel it is unlikely that the grooming and eating seen in the present study were secondary to the elicitation of pain or other strong sensation, since most electrodes produced these behaviors unaccompanied by meowing, crying, hissing, growling, escape behavior, or other responses indicative of pain or unpleasant sensations. Furthermore, it would be difficult to interpret the elicitation of two highly differentiated behaviors, such as eating and grooming, on the basis of a single explanation such as pain. We cannot rule out, however, the possibility of more subtle and specific sensory effects of the stimulation that may have influenced these behaviors.

Histological analysis showed that the effective brain regions for eating and grooming were similar, and included the fastigial nucleus, superior cerebellar peduncle, and the basal vermis (Fig. 1). The effective region was highly localized and surrounded by negative areas laterally, ventrally, and dorsally. While the effective areas for eating and grooming were similar, there appeared to be some fine anatomical differentiation within this region, since 17 electrodes produced only grooming, and two only eating.

The distribution of effective electrodes for eating and grooming corresponds to an anatomical projection, the uncinate tract of Russell, that originates in the fastigial nucleus and exits from the cerebellum through the superior cerebellar peduncle (11). The fastigial nucleus (which receives input from the vermis) projects, through this pathway, to widespread areas of the reticular formation and vestibular nuclei (9–11). This would provide ample possibilities for the projection to influence lower sensorimotor mechanisms such as those for grooming and eating. We were unable, however, to trace the effective region for eating and grooming into the reticular formation with stimulation, perhaps because of the diffuseness of this pathway after leaving the superior cerebellar peduncle. Grooming or eating were not elicited in the present study by stimulation of the dentate or interposed nuclei, or of the superior cerebellar peduncle rostral to the level of the trigeminal motor nucleus. These findings argue against the potential involvement of the massive rostral projections from the deep cerebellar nuclei, which constitute the major portion of the superior cerebellar peduncle.

Cerebellar stimulation has been reported to elicit lip, tongue, and jaw movements, as well as swallowing movements (5, 6). Eating, however, has not been reported, perhaps because most earlier studies were directed toward the determination of more elementary motor responses, and did not provide food or other items that would allow the expression of more complex behaviors that require a goal object. Koella (5) has made a brief reference to "wild biting and licking of the legs" induced by cerebellar stimulation. This behavior may have been similar to the strong compulsive grooming we occasionally observed with high, suprathreshold stimulation intensities.
Stimulation of the Cerebellum

Most electrodes, however, at moderate stimulation intensities, produced more natural-appearing grooming that lacked this compulsive characteristic.

Grooming and eating, including eating of non-nutritive objects, have been elicited by diencephalic stimulation in cats (12–14). The functional relations, however, between the diencephalic mechanisms and the cerebellar systems for eating and grooming are not clear. It is unlikely that the cerebellum is the locus of the lower sensorimotor mechanisms for these behaviors, since cats can eat and groom after total removal of the cerebellum (15). However, the finding that stimulation of specific regions of the cerebellum can induce complex species-characteristic behaviors, such as eating and grooming, suggests that the cerebellum may exert some measure of modulatory control over the sensorimotor mechanisms for these behaviors, perhaps acting in parallel with the influence from diencephalic regions. Further, since the individual components of eating and grooming elicited by cerebellar stimulation were well integrated into coordinated sequences of behavior, it appears that this cerebellar influence is exerted at a fairly high level in the neural organization of these behavioral mechanisms.

A traditional role of the cerebellum is that of improving the coordination of individual muscle movements by a relatively direct action on lower reflex mechanisms. The results of the present study suggest that the cerebellum may also serve to facilitate and coordinate entire sequences of species-characteristic behaviors by acting at higher, more complex, levels of organization in brainstem behavioral systems.

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