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Analysis of the Catnip Reaction: Mediation by Olfactory System, Not Vomeronasal Organ

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Pet owners and behavioral scientists alike are fascinated by unique behavioral reactions that cats show in the presence of catnip. These experiments explored the possibility that the catnip reaction might be triggered by chemosensory stimulation of the vomeronasal organ. In the chewing and mouthing of the catnip source, substances might be dissolved in saliva and transported to the vomeronasal organ. The rolling and rubbing during a catnip reaction might be a sexual response activated by the accessory olfactory system since the system projects to parts of the brain involved in mediation of sexual behavior. However, removal of the vomeronasal organ did not attenuate any of the behavioral reactions to catnip. Olfactory bulbectomy immediately eliminated catnip responding, revealing that the chemosensory stimulus evoking the catnip reaction is undoubtedly mediated through the main olfactory system. Catnip activates behavioral elements associated with several species-specific behaviors, including sniffing and chewing as associated with oral appetitive behavior, rolling and rubbing characteristic of female sexual behavior, batting the catnip source characteristic of play behavior, and a type of kicking associated with predatory behavior. These behavioral reactions occur randomly and intermittently.

Cat owners have been intrigued for centuries at the apparent pleasure cats get from smelling, chewing, and interacting with catnip. Some cats are regularly treated to psychological "trips" by owners who provide them with the dry leaves, catnip-stuffed toys, or objects sprayed with material from aerosol cans of catnip extract.

The catnip reaction characteristically involves first approaching the catnip source, sniffing it for a brief period, and licking or chewing the material. In some cats this is the extent of the response but in others the reaction progresses so that cats rub their cheeks and chin over the catnip source. They then may rub their bodies on the catnip source or on the nearby ground while rolling from side to side. Pawing or digging at the catnip source is also common. There appears to be a satiation of

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the catnip response in that one reaction usually lasts for 5–15 min and cannot be evoked again for an hour or more (Hatch, 1972).

The behavioral similarity between a cat's response to catnip and the rolling and rubbing of female cats during courtship and just after copulation are striking (Palen and Goddard, 1966; Todd, 1963). This has led some investigators to conclude that the catnip reaction activates the neural system in the brain related to the display of female sexual behavior. This is an intriguing hypothesis since chewing of the catnip is a consistent part of the catnip reaction. One could argue that by chewing and mouthing the catnip, substances from the catnip leaves could be dissolved in saliva and transported to the vomeronasal organ (VNO) through the incisive duct by means of a vasomotor pumping mechanism which sucks fluid into the vomeronasal organ. The anatomy of the VNO system and the autonomic control of such a VNO vasomotor pump in cats has been recently described by Eccles (1982). The VNO and the related accessory olfactory system might be considered a logical mediator of the catnip reaction since the projection of the accessory olfactory system is to regions of the brain such as the medial amygdala and medial preoptic area that are closely related to sexual behavior (Hart, 1983; Scalia & Winans, 1975; Wysocki, 1979).

The purpose of this study was to quantitatively analyze the catnip reaction and then to study the effects of VNO removal and subsequent olfactory bulbectomy on the occurrence of the catnip reaction. It had been reported previously (Todd, 1963) that anesthetization of the olfactory mucosa abolished the catnip reaction. However, one could argue that without olfactory attraction or guidance to the catnip source, cats would not mouth or chew the catnip source to expose the VNO to it; and, therefore, rendering an animal anosmic does not reveal whether the reaction is mediated by the accessory olfactory or main olfactory system. By removing first the VNO and subsequently the olfactory bulbs, one could differentiate between mediation by the accessory versus by the main olfactory system.

EXPERIMENT 1

Methods

Subjects. Eight female and six male cats obtained as adults from a random source served as subjects. These were subjects that had proven to be responders to catnip in preliminary tests.

Test procedures. Subjects were adapted to a test enclosure of cloth netting about 1.2 × 1.2 × 0.8 m (upside-down child's playpen). The catnip source was a ball of commercially obtained catnip leaves tied into a gauze wrapping, approximately 2 cm in diameter. The catnip source was anchored to the floor of the test enclosure so that it could not be batted or kicked out of the enclosure. Each test began with presentation

of the catnip source and lasted for 15 min. An observer used an event recorder to note the occurrence and duration of the following reactions: (1) sniffing the catnip source, (2) chewing of the catnip source, (3) rubbing the head, neck, and/or body over the catnip source or rolling on the floor, (4) batting the catnip source as if to play with it, and (5) biting and kicking of the catnip source with the back legs. The test was ended when the cat walked away from the catnip or otherwise ignored it for a period of at least 5 min or at the end of 15 min. Five tests were administered to each subject over a 3-week interval. At least 3 days separated each test.

Results

These subjects were selected for potential to display the catnip reaction. Of domestic cats, only about 50% display the catnip reaction (Todd, 1962). The analysis of five tests on each of the 14 subjects revealed a rather stereotyped responding to catnip. There were five recognizable and consistent behavioral reactions. Sniffing the catnip source after visually orienting upon it and approaching it was usually the first reaction. The mean latency to this behavior from the start of the test was 9.7 s. Chewing the catnip source was usually, but not always, the second reaction and the chewing was with either the incisors or the premolars (Fig. 2). The chewing was at times reminiscent of that of a cat biting into the flesh of a rodent that it had killed (Leyhausen, 1979). A third reaction was rubbing the chin or the side of the face on the catnip, followed by rubbing the neck and body over the catnip or alongside it (Fig. 1). This behavior was virtually identical to that observed in female cats during precopulatory interactions with males and during copulatory after-reactions as observed in tests of sexual behavior. Batting of the catnip ball with one of the forepaws was another common response (Fig. 1). This behavior was reminiscent of that observed when kittens play with balls or fluttery leaves. The above behaviors were observed in all subjects. Of the 14 subjects, 6 exhibited holding the catnip source with the front feet, sometimes biting it, and kicking it with the hind paws (Fig. 1). This pattern is similar to that described for behavior of cats towards rodents prior to killing the prey (Biben, 1979; Leyhausen, 1979). Other reactions sometimes observed were pushing a catnip source around with the nose or carrying it in the mouth around the test enclosure. The above behavioral patterns were virtually the only reactions to the catnip observed during the tests. Flehmen or the gape response previously described for cats and believed to be involved with VNO function (Verberne, 1970) was not observed in any catnip tests.

With the exception of the initial sniffing, the sequencing of these behavioral elements was virtually random as illustrated in Fig. 2, showing a sequence of behavioral elements during one sample 15-min test. The

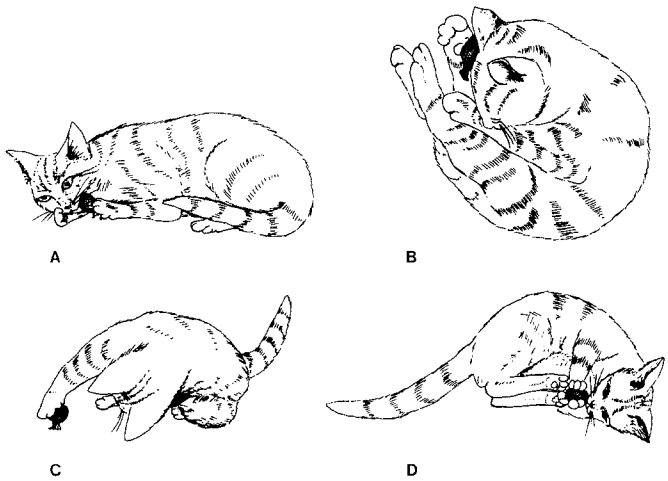

FIG. 1. Behavioral reactions displayed during a catnip bout. Sniffing is not illustrated. The pictures are drawn from motion picture frames. (A) Chewing of a catnip ball, characteristic of oral appetitive behavior. (B) Rubbing and rolling characteristic of female sexual responding. (C) Batting the catnip ball, characteristic of play and predatory behavior. (D) Holding the catnip ball, and kicking it with the back legs, characteristic of play and predatory behavior.

mean amount of time spent by all 14 subjects per test in each behavioral element recorded is presented in Fig. 3.

Discussion

The behavioral elements that were systematically measured in the present study were the same as those described by other investigators of the catnip reaction (Hatch, 1972; Palen & Goddard, 1966; Todd, 1963). The head–body rubbing and rolling has been emphasized as especially prominent, probably because it is so easily associated with sexual re-

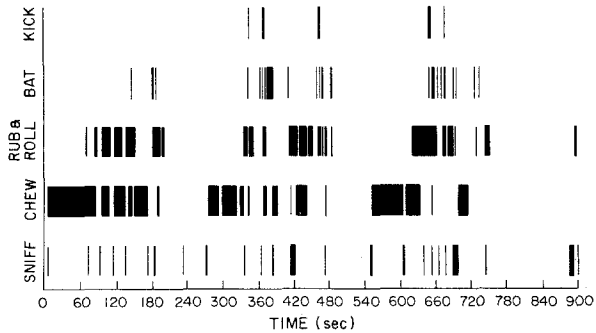

FIG. 2. Typical intermittent sequence of catnip behavior reactions during a 15-min test on one subject.

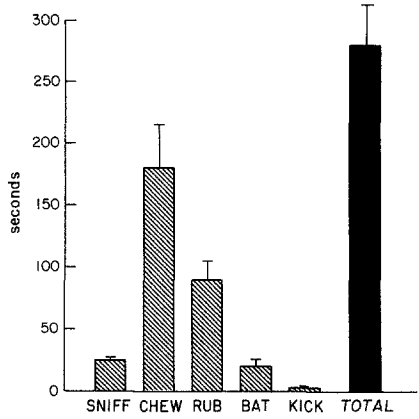

FIG. 3. Mean duration of time spent by subjects in each catnip behavioral reaction in baseline tests. The bar for total time represents any interaction with the catnip source and is shorter than the sum of all other bars because some reactions occurred simultaneously.

sponding in female cats. In the present study more time was spent in rubbing and rolling than in batting or kicking. However, neither the present study nor those of others have reported the display of other aspects of female sexual behavior such as pelvic elevation, leg treading, and tail deviation. Since catnip evokes elements of behavioral systems that one could associate with oral appetitive behavior, play behavior, and predatory behavior, as well as female sexual behavior, it is not logical to associate the catnip response with the elicitation of sexual behavior only. It appears as though the active ingredient of catnip evokes elements of several species-specific behavioral systems almost at random, and that the ingredient loses its potency to stimulate these systems after 5–15 min of exposure.

EXPERIMENT 2

The tests of Experiment 1 served as the baseline tests for this experiment. Half of the subjects ($N = 7$) were next subjected to the removal of the VNO (VNX) and half ($N = 7$) to a VNX sham operation (VNX-SHAM). When it was learned that the VNX subjects continued to respond after extensive postoperative testing, four of these and three VNX-SHAM subjects were subjected to olfactory bulbectomy.

Methods

To eliminiate VNO input without disturbing main olfactory function, an operation was developed to remove the entire VNO by dissection through the hard palate. The operation was similar to that employed by others with guinea pigs (Beauchamp, Martin, Wysocki, & Wellington, 1982). All subjects were anesthetized with induction by a ketamine–

acepromazine mixture, intubated, and maintained in surgical anesthesia with fluothane. With the subject lying in dorsal recumbency, the incisive ducts were located just behind the incisors and longitudinal incisions were made directly caudal to the ducts. The edges of the epithelium were spread and a pneumatic bone drill was used to carefully remove vomer bone overlying the VNO cartilages. The cartilages, and the VNOs contained within, were carefully dissected from surrounding tissue, pulled forward, and cut from the incisive ducts. The epithelium was closed with absorbable suture, and the cats were allowed 1 week to recover before testing commenced. There appeared to be no disturbance of the cats' investigative behaviors from the operation, and all subjects were willing to chew food the day after the surgery. The sham operation consisted of making an incision in the epithelium overlying the hard palate and using the pneumatic bone drill to cut into, but not through, the hard palate overlying the VNO. The incision was closed as with the VNO removal.

The olfactory bulbectomy was performed as described elsewhere (Hart, 1981) after the subjects had been anesthetized as for the VNO removal. Briefly, the area of the skull overlying the frontal sinus was exposed through a skin incision and an opening into the roof of the frontal sinus made with a pneumatic bone drill. The medial septum of the frontal sinus was then removed and an additional hole in the floor of the frontal sinus was made to expose the olfactory fossa containing the olfactory bulbs. The bulbs were aspirated through a metal tube and the olfactory tracts were completely severed by aspiration.

Anosmia was verified 1 week after the operation by means of a hidden food test. In this test a gauze sponge soaked in tuna juice was placed under 1 of 3 paper towels placed on the floor and the subjects were allowed to explore the floor. Normal cats can smell the tuna and go directly to the correct towel. Anosmic cats typically walk directly over the towels, including the one covering the tuna. All bulbectomized subjects proved to be anosmic, whereas VNX subjects went directly to the correct towel.

The tests for catnip reactions were identical to those used in Experiment 1. The last 4 tests of Experiment 1 served as the baseline tests. There were 20 postoperative tests administered in the 11 weeks beginning 1 week after the operation. When it was learned that VNO removal did not immediately diminish catnip responding, it seemed conceivable that changes in behavior might be evident after a more prolonged period, as had been reported for the loss of head bobbing in guinea pigs after VNO removal (Beauchamp et al., 1982). Therefore, subjects were allowed a 10-week rest with no exposure to catnip before being given an additional 10 tests over 5 weeks. These latter 10 tests served as baseline tests for the olfactory bulbectomy. Following the olfactory bulbectomy or sham

operation, an additional 5 tests were conducted over the subsequent 3 weeks.

At the conclusion of the experiment the completeness of olfactory bulbectomy was verified by gross dissection and the completeness of the VNO removal was verified by histological sections taken through the nasal septum and hard palate after decalcification.

Results and Discussion

All subjects displayed sniffing, chewing, rubbing and rolling, and batting at least once in tests conducted after VNO removal. Four VNX and five VNX-SHAM subjects engaged in kicking in postoperative testing. The mean duration of time subjects spent in each behavioral pattern before and after VNO removal is given in Table 1. The total mean time spent by subjects interacting with the catnip source is presented in Fig. 4. There was no decrease in total time spent interacting with the catnip source and no significant change in time spent engaging in any particular behavior pattern in the postoperative testing extending 27 weeks following VNO removal. Olfactory bulbectomy, however, virtually eliminated the catnip responding immediately in all seven subjects as illustrated in Fig. 4. This was a significant effect ($p < .01$, Wilcoxon matched-pairs signed-ranks test).

This experiment provides fairly conclusive evidence that the catnip reaction is mediated by the main olfactory system with little or no participation from VNO input. This documentation of the importance of the olfactory system in mediating the catnip reaction is consistent with the previous report by Todd (1963) that anesthetizing the olfactory mucosa abolished the catnip reaction.

GENERAL DISCUSSION

Some of the theories regarding the explanation for the catnip reaction have related the similarity of the reaction to that of female sexual behavior.

TABLE 1
Mean (± SEM) Duration of Time(s) Spent per Test by Subjects in Each Behavioral Element before and after VNO Removal

	N	Sniffing	Chewing	Rubbing and rolling	Batting	Kicking	Combined
				Preoperative			
VNX	7	28 ± 5	134 ± 20	112 ± 35	25 ± 10	1 ± 1.3	265 ± 26
VNX-SHAM	7	19 ± 4	231 ± 55	70 ± 16	11 ± 3	3 ± 2	300 ± 60
				Postoperative			
VNX	7	22 ± 4	161 ± 35	61 ± 16	12 ± 4	2 ± 1	201 ± 31
VNX-SHAM	7	12 ± 1	259 ± 58	67 ± 20	14 ± 4	1 ± 1	318 ± 59

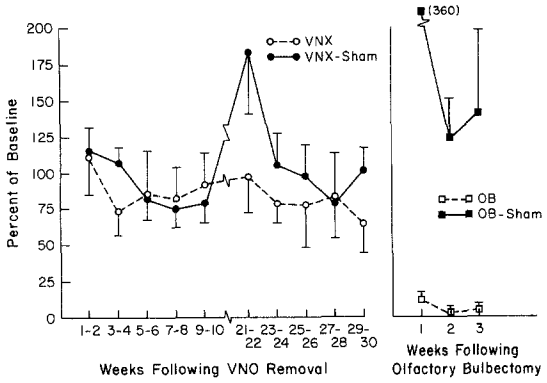

FIG. 4. Effects of vomeronasal organ removal (VNX) or olfactory bulbectomy (OB) on catnip responding. Graphs show total time spent interacting with the catnip ball as a function of percentage of baseline tests.

One notion is that catnip coincidentally mimics one or more of the substances found in male cat urine which normally elicits rolling and rubbing in female cats (Todd, 1963). Others have argued that perhaps both catnip and estrogen alter the skin sensitivity of a cat's head and body and that rubbing and rolling provide relief (Palen & Goddard, 1966). A different line of reasoning is that catnip produces a "pleasure" response unrelated to sexuality, more like that produced by psychedelic drugs, and that this is expressed in the rubbing and rolling (Hatch, 1972). None of the above theories received much support in the present study in that catnip activated behavioral elements associated with several species-specific behaviors including sniffing, chewing as associated with oral appetitive behavior, rolling and rubbing characteristic of female sexual behavior, and a type of kicking seen in play and predatory behavior. The behavioral reactions occurred randomly and intermittently except that sniffing was usually displayed first. One could argue that catnip responding represents the activation of the neural circuitry of several species-specific behavioral patterns. This is a view consistent with that of Hill and co-workers, who studied the reactions of several felid species (Hill, Pavlik, Smith, Burghardt, & Coulson, 1976).

Inasmuch as olfactory bulbectomy, but not VNO removal, eliminated catnip responding, it must be concluded that the chemosensory stimulus that evokes a catnip reaction is mediated through the main olfactory system. VNO removal did not attenuate any of the behavioral reactions nor the total time spent responding to the catnip source. This was true even in prolonged testing for 6 months after VNO removal, thus ruling out a gradual reduction of a VNO-mediated reaction as reported for head bobbing in guinea pigs (Beauchamp et al., 1982). The VNO is strongly implicated in flehmen behavior in that flehmen is believed to be involved

in transporting fluid-borne stimulants to the VNO (Hart, 1983) and male cats do display flehmen during sexual encounters with females (Verberne, 1970). The fact that flehmen was never seen when the subjects were interacting with catnip also is consistent with the notion that the VNO is not involved with catnip responding.

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