

INHERITANCE OF THE CATNIP RESPONSE IN DOMESTIC CATS

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AN ESSENTIAL oil, nepetalactone, was isolated from the catnip plant (*Nepeta cataria*) by McElvain *et al.*^{2, 3, 4} and Meinwald⁵. McElvain² demonstrated with lions that the oil is the substance which is responsible for the attraction of cats to the plant and the only constituent capable of inducing a response.

This familiar response has been broken down into four components, *viz.*, 1) sniffing, 2) licking and chewing with head shaking, 3) chin and cheek rubbing and 4) head-over roll and body rubbing. None of these automatisms is unique to catnip, each of them apparently belonging normally to sexual or ingestive behavior¹. These components almost invariably appear in the above sequence. In fact, among 58 responding cats, all tested with dried leaves, only three individuals deviated from this sequence and omitted the licking and chewing with head shaking. These animals went immediately into the rolling phase, which seemed to be exceptionally violent. Component four may last from three to six minutes before all response is extinguished. Additional behavior patterns noted occasionally are claw sharpening and washing, both of which occur as displacement activities in the ethological sense in sexual behavior¹.

Among responding animals the response may occasionally be inhibited for obscure reasons, necessitating repeated testing of non-responders before drawing conclusions. Also, the response is not manifested in kittens under six to eight weeks of age and may not develop fully until three months of age. In fact, catnip often produces a distinct avoidance response in young kittens which is gradu-

ally replaced by indifference in non-responders and by heightened curiosity in responders. Whether nursing is in any way connected with inhibiting the response has not yet been determined. In one case a six- to seven-week-old nursing kitten gave a total response, but this seems exceptional. A distressed or enraged animal may still respond, and neutering appears to have no effect on behavior towards catnip.

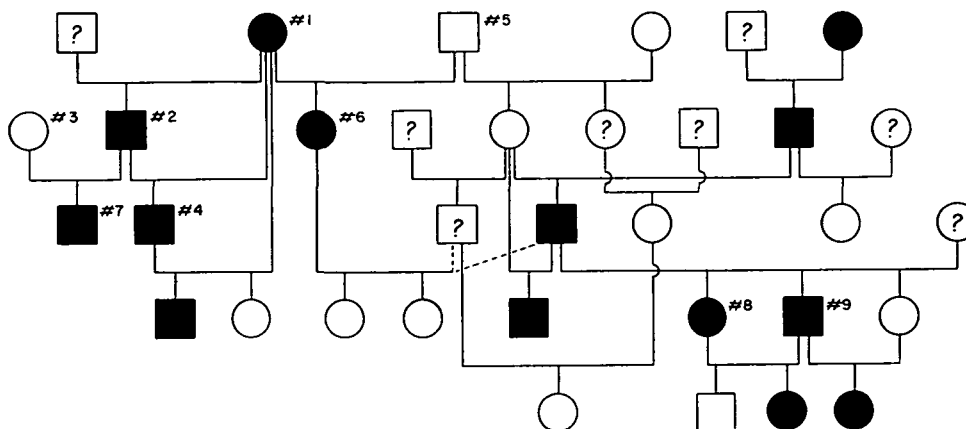
Methods

On an irregular basis, cats in the colony were offered dried catnip leaves over a period of several years. It was initially noted that some animals never responded while others responded rather consistently. The first step taken was to tabulate responders and non-responders among the related cats in the colony and to extend the pedigree to include animals from outside the colony which were occasionally used as studs. In this instance it was possible to gather information on many other animals sired by these studs since they were Siamese cats mated under strict supervision of a fancier[†]. It is from this pedigree alone (Figure 5) that the genetic basis has been determined, but future crosses can now be designed in order to obtain statistical support for the mode of inheritance suggested by the pedigree.

Administration of the catnip has usually been effected by presenting dried leaves directly to the subject. Some animals were tested with nepetalactone-containing atmospheres in an olfactometer, the details of which will be reported more fully in a future paper. Suffice it

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A PEDIGREE OF CATNIP RESPONSE

Figure 5

Solid forms represent catnip-sensitive cats, open forms non-sensitive cats, and question marks sensitivity of cats not yet determined. Dotted lines indicate questionable paternity. See text for discussion of pedigree numbers.

to say that the concentration of the substance effective in eliciting a response is extremely low, perhaps as low as one part in 10^9 - 10^{11} . Chewing is not always present in cats tested under these conditions, and licking with head shaking is not as pronounced.

Results

From the pedigree, the significant crosses will be seen to be those of animals No. 1 \times No. 4 and No. 8 \times No. 9. In both cases two responders have produced a non-responder, indicating a dominant factor controlling the response. Among other contributions of the pedigree is the exclusion of sex linkage. For example, responding as a sex-linked recessive is precluded by the cross No. 1 \times No. 5, and responding as a sex-linked dominant is precluded by the cross No. 3 \times No. 2.

The symbols chosen for this characteristic are +ⁿ for responders or nepetalactone-sensitive cats and n for non-responders or non-nepetalactone-sensitive cats. The rather arbitrary designation of responding as the wild-type is based principally on the supposition that non-responding is the absence of some undefined sensory or neural function. With respect to gene frequency some introductory work has

been started*. These data are summarized in Table I. The combination frequencies are approximately .69 for responders ($p^2 + 2pq$) and .31 for non-responders (q^2). The gene frequencies calculated from these figures are approximately .45 (p) and .55 (q). It should be noted that due to an inability to test all cats under equivalent conditions and to repeat the testing procedure, the value for responders must be taken as a minimum. It is tentatively as-

TABLE I. Response category distribution in 84 cats tested with catnip. Bracketed figures indicate the number of neutered animals included in the figure preceding the brackets.

Maximum stage of response	♀ ♀	♂ ♂	Totals
Sniffing	5	3	8
Licking and chewing	13 [2]	18 [1]	31
Chin and cheek rubbing	1	0	1
Head-over-roll, etc.	7*	11 [1]	18
Total responders	26	32	58
Non-responders	15 [1]	11 [2]	26
Totals	41 [3]	43 [4]	84

*Three animals from this group omitted licking and chewing.

*The animals used in the survey work are in no way related to those in the pedigree discussion above. The group consisted of strays, etc. housed at the Angell Memorial Hospital, M.S.P.C.A., Animal Rescue League, and Massachusetts General Hospital, Boston, to which organizations I wish to express my thanks for their cooperation. No surgical cases or diseased cats are included in the data analyzed with respect to the catnip response. Evidence will be presented in a future paper to show that this sample is drawn from a random breeding population.

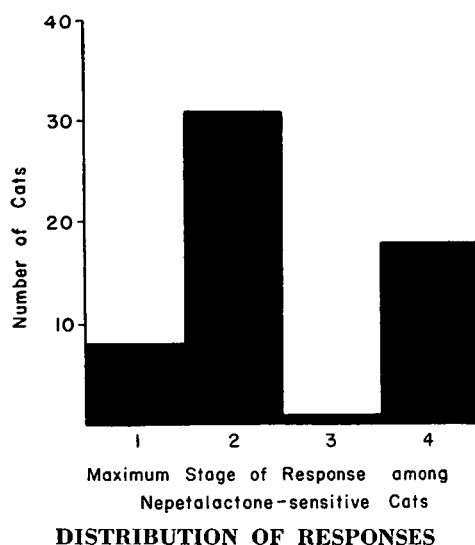


Figure 6

The above chart shows the four classes of catnip response: 1) sniffing; 2) licking and chewing with head shaking; 3) chin and cheek rubbing; 4) head-over roll and body rubbing.

sumed that some partial responses are due to various inhibiting factors resulting from the temporary and recent caging of these animals in strange surroundings and in the vicinity of strange cats. Nevertheless, among one group of cats tested (data not included) normal responses were noted in some individuals that had been moved a distance of several miles in crowded cages with strange animals. They fought with one another violently in the cages, objected to being removed to the testing chamber and started at even the slightest movement. In addition, some of these animals had been severely light-deprived from birth (as little as 40 hours total illumination in 28 weeks).

The eight animals grouped under sniffing are considered responders on the basis of the rather compulsive and prolonged sniffing which they displayed. In testing a number of cats with tea leaves no extensive sniffing was observed. Further work is necessary to clarify the rather unusual observation that only a single cat which failed to give a total response did manifest chin and cheek rubbing. There appear to be two classes of responders (Figure 6), partial and total, but it is impossible to separate a possible genetic basis for this from environmental factors without a uniform testing situation. With the exception of the three individuals noted, all cats passed through the stages preceding their maximum stage of response. The degree of responding does not correlate with the homozygous and heterozygous condition as judged from the pedigree since known heterozygotes,

No. 6 and No. 7, gave total responses. Thus, polygenic modifiers may be indicated (expressivity). The present data do not warrant any conclusions as to the degree of penetrance. There is no significant difference between males and females as determined by a χ^2 homogeneity test ($\chi^2 = 1.18$, $P = ca. .70$). Stages two and four appear to be stable while one and three lead to further reaction. Whether any individual cat may fluctuate on different occasions from stage two to stage four is not known, although it appears that they are consistent under a given set of circumstances. Also, there still remains the objection that the categories of response are not quantitative and may be more apparent than real in indicating response intensity.

Finally, the behavior of the alternatives "+" and "u" with respect to several other known loci in the cat has been studied as far as possible from the pedigree and the survey animals to determine whether linkage does occur. From the pedigree it appears that this factor is independent of Manx, Siamese, tabby and agouti, on the basis of its distribution in the progeny, assuming that crossing-over is not significantly involved. However, the latter possibility still exists since the data are small. From the survey cats there appears to be no correlation to white spotting, blue dilution, polydactyly or long hair. Of course, in this small group recombinant chromosomes of various types might completely mask any linkage effect, which only future breeding will resolve.

Summary

Four behavioral components of the catnip response are described briefly. The analysis of a pedigree indicates that responding is inherited as an autosomal dominant. Other aspects of inheritance of the catnip response are discussed.

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