pletely immobilized and the recovery time was relatively longer. If the dosage was increased to 0.3 μg, the flies were completely paralyzed and there was never any recovery. Similar curves for *Sarcophaga bullata* and *Phormia regina* closely resemble this curve.

Preliminary experiments with the cockroach *Periplaneta americana* give an indication of its dose response. Injection of 0.1 to 0.4 μg brings no response; 0.5 to 0.9 μg has a partial effect whereby one pair of legs is paralyzed, depending upon the site of injection; there is some drooping of the head and sluggishness in movement. Injection of 1.0 to 1.4 μg has an intermediate effect, with general partial paralysis and very sluggish response to stimuli; paralysis of the limbs at the site of injection is complete, but the animal never completely loses the ability to move. Doses between 1.6 and 1.8 μg effect complete flaccid paralysis. From three to seven insects were tested in each dosage range and all completely recovered. A curve of dose response relative to recovery time has not yet been worked out for cockroaches as they are extremely slow to recover; there is also a much longer time lag between injection and the first appearance of effects. There is, however, a definite relation between dose and severity of the paralysis.

According to Goodman and Gilman (*3*), the mode of action of *d*-tubocurarine chloride is one of competition with acetylcholine for acceptance by the cholinergic receptors of the motor end plate, with no depolarization of the cell membrane and consequently no contraction of the muscle fiber. Workers indicate that curare has no effect on insect neuromuscular junctions or neuromuscular transmission (*1–3*).

The obvious difference between our study and earlier work is that Roeder (*1*) and others used a dosage, ranging from 10^{-3} to $10^{-7}M$, that works very well in vertebrates but produces no detectable syndrome in insects. Higher doses of curare do produce a typical effect in the insects so far studied.

Quite obviously there is no direct correlation between body weight of the insects and the dosage of curare required to produce paralysis (Table 1): the Coleoptera, *Epicauta*, weighing 283.1 mg, requires only 0.069 μg/mg for complete paralysis, while a cockroach nymph (*Periplaneta americana*), weighing 270 mg, requires 1.11 μg/mg to show only partial paralysis. And *Acheta*, weighing approximately the same as the cockroach nymph, showed only a partial effect after a dose of 0.279 μg/mg.

The extremely high dosage required to paralyze insects may reflect a number of factors, all of which remain conjecture. Quite obviously curare works as a paralyzing agent in insects, and it will be of significant interest to determine the site of action and type of chemical response at the cellular level.

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4. Assisted by NSF grant GB-2833 and by the U.S. Air Force (grant AFOSR 889-65).

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18 February 1966

Seasonal Variation in Mating Behavior in Cats after Desensitization of Glans Penis

Abstract. *The glans penis in 14 sexually experienced cats was desensitized by section of the nerves dorsalis penis. These males mounted the estrous female readily but they were so disoriented that they could not achieve intromission. Reduced sensory feedback resulting from the operation and from lack of intromissions caused a decided drop in sexual activity in the fall with recovery in early winter. A latent sexual cycle in male cats is revealed, which corresponds in time to the established female cycle.*

In the comprehensive theory of the regulation of mammalian sexual behavior developed by Frank Beach (*1*), the sensory input into the system is considered nonspecific and additive. This conclusion, which was derived from his own research on rodents and from a survey of the literature (*2*), stems from a variety of observations and experiments that show that sensory deprivations (visual, auditory, tactile from snout and genitalia), regardless of modality or area, cause a decline in sexual activity, but do not cause qualitative changes in sexual behavior. Conversely, increasing the stimuli derived from the sexual partner or from the environment increases sexual activity, while the gonadal hormones and neural activity, particularly of the neocortex, adjust the threshold for appearance of the various behavioral acts.

In 1962 we reported (*3*) preliminary observations on a sensory deprivation in male cats, observations that seemed, at first thought, to be at variance with this part of Beach's theory. By surgical procedure the nerves dorsalis penis of several males were severed bilaterally. This operation desensitizes the glans penis but does not interfere with erection. These males showed no observable decrease in sexual activity. They mounted the female as readily as before operation but were so disoriented that they were unable to insert the penis into the vagina. Thus, by a small circumscribed sensory deprivation we produced major qualitative changes in behavior with no immediate loss in sexual arousal. As testing continued, however, decrements in sexual behavior appeared; not as a continuous decline, which would be predicted from Beach's theory, but as a pronounced seasonal decline in the fall with a return to higher levels of sexual activity in the winter.

We are now presenting an interim report of this experiment based on the behavior of 14 male cats that have been observed for 2 to 26 months after operation (average 18 months). Seven of these males are still being observed. The subjects were domestic short-hair males of unknown ancestry. Seven were obtained as adults and were presumed to have had sexual experience. The other seven were obtained as kittens and raised in laboratory cages, and all of the mating activities of these animals were controlled and observed. Since our analysis is not concerned with the effects of experience, and since there were no apparent differences in sexual behavior between the two groups, the data of the two groups were pooled.

Sex tests and methods of observation were similar to those used by Rosenblatt and Aronson (*4*). The major items of the normal mating pattern observed are (i) the male grips the back of the female's neck with teeth; (ii) mounts the back of the female; (iii) makes stepping movements with hind limbs; (iv) exhibits pelvic thrusting which is followed by (v) a single brief intromission with ejaculation after which (vi) the male dismounts. The females used as test animals were spayed and brought into heat by weekly injections of 0.15 mg of estrodiol benzoate in 0.15 ml of sesame oil. All males were given a 20-minute sex test in a specific test room once a week except for occasional gaps resulting from fortuitous circumstances. They were given 5 to 86 tests prior to operation (Table 1) and had from 8 to 58 intromissions. The preoperative records thus served as control data.

Under nembutal anesthesia, sections of the nervus dorsalis penis, about 3 mm in length, were removed along with equivalent portions of the accompanying dorsal arteries (Fig. 1). To be sure that removal of the dorsal blood vessels or other surgical procedures did not interfere with penile function, we performed a sham operation on an additional male, removing the dorsal arteries but leaving the dorsal nerves intact. Intromission occurred in six successive postoperative tests, and no decrements or changes in behavior were observed.

None of the animals achieved intromission during the first 1½ months after operation, and in ten subjects this loss continued as long as the animals were tested. In two males, HA and RO, intromissions reappeared after 6 and 18 weeks, respectively. Two animals still being tested (PH and OD) show occasional intromissions.

Failure to achieve intromission was correlated completely with improper orientation of the male on the back of the female during the mount. At most times the pelvic region of the male was so far forward and highly elevated that the penis seldom came near the genital area of the female. In four animals disorientation was much more profound. By 13 weeks after operation, TM developed the habit of lying on his side while holding the neck-grip. In this position he would thrust vigorously with his penis several centimeters from the female. Male RO (during the first 14 postoperative weeks) and male MV would circle the female in a frenzied manner while holding the neck-grip. These males were frequently observed thrusting vigorously while standing at right angles to the female. These abnormal patterns were never observed prior to operation. With PH and OD, the cats that intromit occasionally, disorientation is less pronounced.

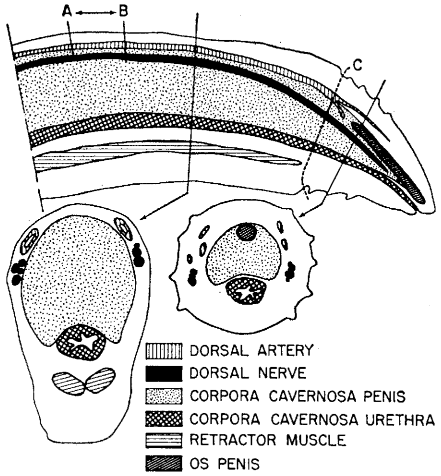

Fig. 1. Diagram of cat penis showing relation of dorsal artery and nerve to the corpora cavernosa. Lines *A–B* show segment of nerve removed. Attachment of prepuce is indicated by line *C*.

After operation, with the loss of intromission, the duration of mounting increased markedly. This usually took the form of long, protracted mounts, many lasting the full 20 minutes of the test period. The behavior of a few males was characterized by a large number of shorter mounts from momentary to a few minutes.

Stepping behavior did not change in any animals. Pelvic thrusting remained vigorous in most subjects, but declined in forcefulness in two. At 6 weeks we noticed in PG that thrusting was less vigorous. By 4 months thrusting was reduced to occasional twitches of the thigh muscles. This change was readily demonstrated by comparing motion pictures taken at 3 and 22 months after operation.

Before operation most of the males would bite the skin on the back of the neck and hold this neck-grip as long as they were mounting. After operation a small number of males would occasionally release the neck-grip during the mount and then retake the neck-grip after a few seconds or minutes, particularly when the female started to move forward. The amount of neck-licking did increase postoperatively but this was related to the fact that the duration of mounting was so much greater and was not attributable to any qualitative change in behavior. No other change in neck-grip behavior was observed in any of the 14 subjects.

Since the dorsal nerves of the penis carry some sympathetic nerve fibers, an important question raised in this study is whether our surgical procedures not only anesthetized the penis but also interfered to some extent with erection. This has been answered in three ways:

1) Examination of the neuroanatomical and neurophysiological literature (*5*) shows that erection is controlled by the pelvic nerve (nervus erigens) and not by the pudendal nerve from which the dorsal nerve of the penis arises (*6*).

2) Occasional observations of erection were made in some of the experimental animals when they lay on their sides during a mount. In all instances erection seemed complete.

3) In five additional males, K. K. Cooper (*7*) performed sacral laminectomies and stimulated the ventral roots of S_2 bilaterally. With the use of a square-wave stimulator at a pulse frequency of 20 per second and of 0.4-msec duration, the voltage was adjusted (from 0.25 to 20 volts) to produce protrusion and full erection within 1 minute of stimulation. After erections had been elicited several times in this manner, the dorsal nerves were sectioned. With the same stimulus parameters as above, the ventral roots of S_2 were again stimulated. Full erection occurred as rapidly as before nerve section in all five subjects. Completeness of nerve section was verified histologically in each case.

Completeness of the denervation of the glans was determined in two ways: (i) The penises of the seven males in which observations had been terminated were sectioned serially and were stained by the Bodian silver-proteinate–gold-chloride technique. In three, frozen sections were also made near the tip of the glans and were stained by the method of Winklemann (*8*). Bundles of functional nerves were seen in RO and HA, the two males in which normal sexual behavior had returned, indicating incomplete surgery or regeneration, or both. In three cats, SY, TM, and PG who never intromitted after operation, the nerves were absent distal to the site of operation except for a few scattered fibers that may represent anastomoses with the nerve cavernosus. In the two others animals (LI and BG), who also did not intromit after desensitization, some nerve bundles were seen distal to the operation and in LI definite signs of regeneration through the scar tissue were evident. Apparently desensitization of the glans were sufficient in these two animals to preclude the return of normal sexual behavior. (ii) Terminal operations were performed on three animals by K. K. Cooper. The dorsal nerve of the penis was exposed deeply, just distal to its origin from the pudendal nerve. Action potentials were displayed on a cath-

Table 1. Summary of tests.

Animal	Preoperative			Postoperative		Date of operation (week of year)
	No. of tests*	Intromissions: Total No.	Intromissions: Average in last 5 tests	No. of tests	Intromissions (total No.)	
BG†	15	21	1.8	52	0	39
CG	47	28	1.0	105	0	10
HA†	86	73	2.6	11	7	13
LI†	12	23	2.6	84	0	11
MV	6	17	3.4	95	0	15
OD	9	20	2.6	86	6	27
PG†	24	28	2.0	85	0	9
PH	6	8	1.4	98	9	13
RO†	43	36	2.0	24	6	26
RS	39	40	1.4	70	0	41
ST	5	12	2.8	64	0	39
SY†	9	12	2.1	14	0	24
TM†	24	58	2.4	80	0	27
WD	11	23	2.2	87	0	29

* Starting from first test in which mounting occurred. † Postoperative observations on these animals have been terminated.

ode ray oscilloscope with bipolar electrodes. In PG and BG, increased firing could not be obtained when the glans penis was stimulated with a camel's hair brush. When the electrodes were shifted to the scrotal branch of the pudendal nerve, stimulation of the scrotum gave a marked increase in firing. In RO, a male in which regular intromissions returned, increased action potentials were readily elicited by stimulation of the tip of the glans.

From the foregoing evidence we cannot claim complete desensitization in any of our 14 subjects, but the evidence clearly demonstrates an extensive and persisting decrement in glans sensitivity in all but two of our subjects examined so far.

Rosenblatt and Aronson (*4*) devised an index figure (sex score) based on the highest level of sexual activity reached in a given test. The median sex score of all the animals for the last five preoperative tests was 10, which indicates two intromissions. After operation, the scores were 8 or less (no intromissions) in all tests except for the four males where intromissions returned.

A striking feature of the level of sexual activity when followed over many months is its cyclical fluctuation. Regardless of the week of year that the operation was performed (Table 1), the sex scores were high in winter and spring (Figs. 2 and 3). They dropped precipitously in late summer (around the 35th week of the year) and rose again in the early winter (around week 50). All except one animal showed this cycle, and eight of the males that were tested for 2 years showed two similar cycles. It is also of interest that in PH and OD, the two animals that have occasional intromissions, these only appeared during the months of high sexual activity.

Analysis of the total duration of mounting per test reveals the same phenomenon, namely, a decided decline in mounting from late summer to early winter (Fig. 2). This period of minimal sexual activity corresponds to the cycles obtained by the sex score, but not precisely in most cases.

Mount latency, the time from the beginning of the test to the first mount, may be used as an additional measure of level of sexual activity, where high latencies reflect low levels of arousal. Here again we found a clear-cut cycle in all subjects except BG and PG. While the peaks in latency correspond to the troughs in mount duration and sex score, the overlap is not exact in most cases (Figs. 2 and 3).

Five different sexual functions can be attributed to the penis of the cat, namely: (i) transfer of semen; (ii) stimulation of the female; (iii) provide sexual stimulation leading to ejaculation; (iv) orientation to the female while mounting; and (v) sensory feedback for the maintenance of sexual arousal.

The first function is obvious and well established. The second is equally clear since the female issues a loud, characteristic cry at the moment of intromission, and then becomes highly resistant to the male. Also, the act of intromission will cause an intact female to ovulate (*9*). The third function, well established for some mammals is presumably true for cats also. While ejaculation has been obtained in physiological experiments, it has not been observed during copulation in the cat as a discreet act separable from the brief intromission. Smears taken from the penis of the tractable nerve-cut males during a mount or immediately thereafter usually had some sperm, but we cannot be sure that their presence represented a normal ejaculation. The fourth, namely, orientation to the female while mounting has not been recognized heretofore as a function of the penis. The only other indication of this function that we could find in the literature is a Swedish veterinary report describing the failure of a bull to achieve intromission following pathological degeneration of the pudendal nerve (*10*).

The fifth, namely, sensory feedback for the maintenance of sexual arousal, is equally new. A test of this hypothesis was actually the major reason for the experiment. We had predicted, after denervation, a gradual decrease in sexual activity similar to that in castrated cats rather than cyclical fluctuations. It is commonly believed that intact male cats are ready to mate throughout the year (*11*). There is limited evidence, however, that some may be slightly less active in the fall (*12*). In the present experiment, data of two intact control males tested for 1 year and 1½ years, respectively, are available. The sex scores of one declined slightly during the fall of two successive years, but in the other no cyclical changes are evident. We have, in addition, evidence from previous experiments (*4*) on four postpuberally castrated males that persisted in high levels of sexual behavior for one to two full years after operation. PW had mount latencies of zero or nearly zero for 2 years; AP and MK for 1 year. The latencies of SV started high after operation and then declined to zero or nearly so and stayed at this level for over a year. The sex score for PW declined from 10 to 8 over a 2-year period. In 1 year, AP went from 13 to 8; MK went from 7 to 4; and SV stayed between 8 and 10 in most of the tests. In none of these data were there any indications of a cycle.

Wild felines, like most mammals, have a definite breeding season (*13*). The wildcat of Scotland, for example, breeds only in the spring. Under domestication, seasonal breeding in many mammals largely disappears (*14*). The domestic cat certainly breeds all year around, especially in captivity (*11*), but a vague cycle attributed to the female does seem to persist, showing heightened activity in the late winter and spring with a lull in the fall. Based on histological and physiological evidence, Foster and Hisaw (*15*) identified, in the case of the female cat, an anoestrus period, extending from September to January, and this has been related to variations in day length. This period coincides fairly well with the time of low activity found in our males. Our experimental desensitization of the penis has apparently brought out a comparable latent cycle in the male. As a working hypothesis we recognize two processes necessary for the maintenance of high levels of mating behavior in the male, namely, (i) environmental influence, especially variations in day length impinging on the neuroendocrine mechanism controlling sexual behavior, and (ii) sensory feedback from the penis (especially during mounting and intromission) acting on the central mechanisms for sexual arousal. When either one or both of these processes are fully operative, high levels of sexual behavior are evident, but when both processes are minimal, a definite lull in sexual activity occurs.

We had expected that our desensitized animals would decline in sexual behavior in a manner somewhat similar to those of castrated males, particularly those that continued to mate for a great many months after operation. This expectation was based on the fact that castration results in structural changes of the skin of the glans (*16*), which may mean lowered sensory input. This prediction was realized in part for our desensitized males. One of them, BG, ceased all sex behavior after 8 months; in three, pelvic thrusting became minimal; after the low period, six males never quite reached the level of total mounting time shown just after operation. A qualitative decrease in sexual excitability was clearly evident in PE, LN, and MV. If there is a real loss in penile sensitivity after castration, it probably occurs gradually in the long-persisting animals. Eventually it is accompanied by loss of erection, which further decreases penile stimulation, so that in the long run loss of feedback may be greater in castrated animals than in our operated animals. This accounts, in part, for the greater loss in arousal which eventually occurs in most castrates.

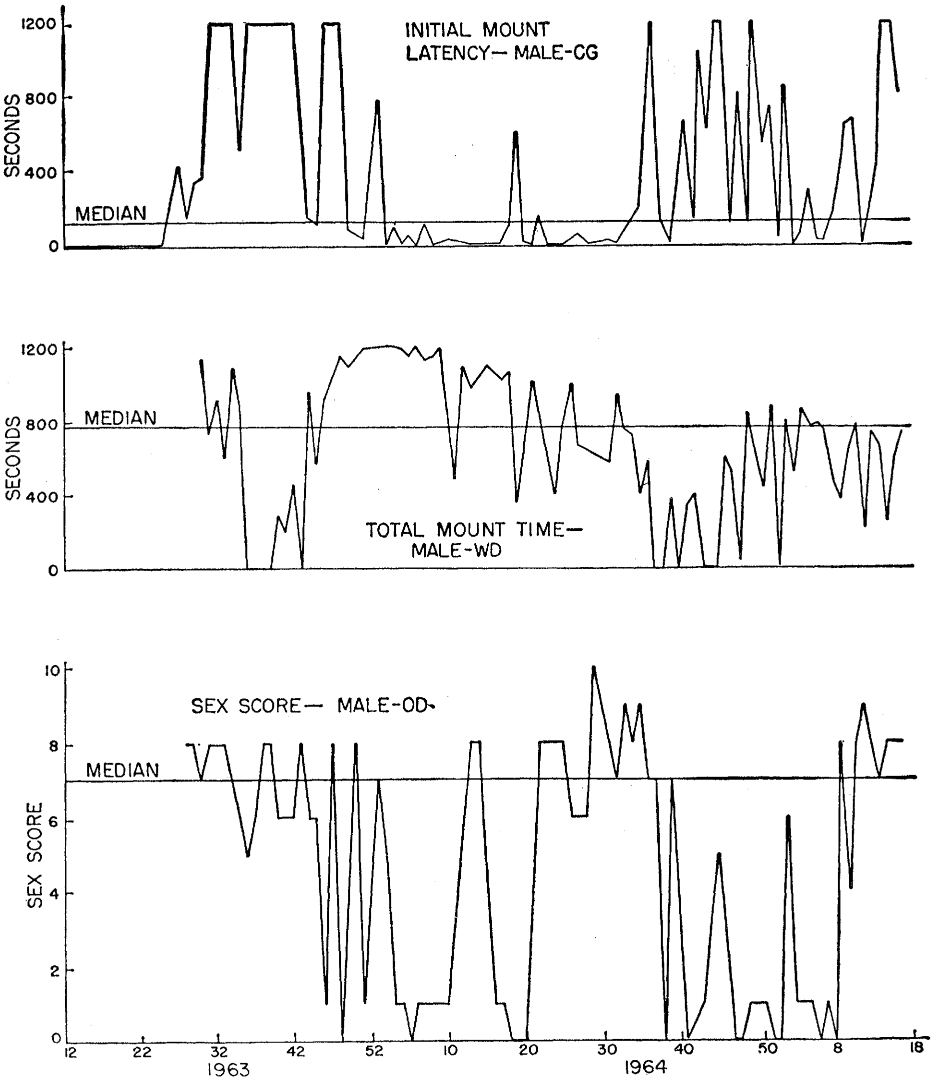

Fig. 2. Samples of complete postoperative records of three quantitative measures for three different males.

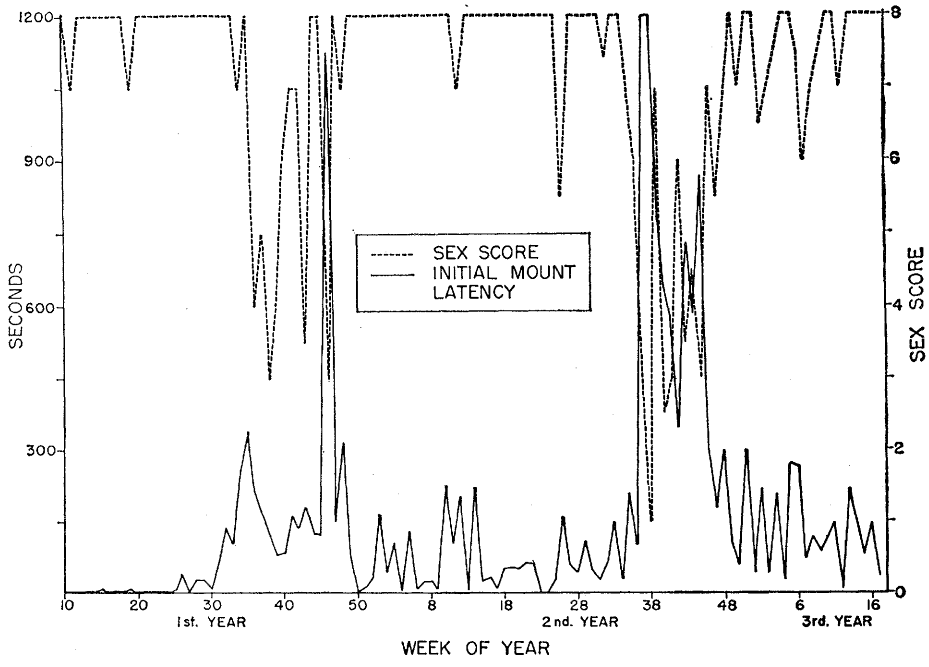

Fig. 3. Median sex scores and initial mount latencies for all tests of all males showing cyclical decline in sexual activity in the fall of each year.

After the publication of our original abstract, two reports have appeared on the use of topical anesthetics on the glans penis of rats, resulting in a loss of intromission and apparently incomplete erection. One report (*17*) indicated no loss of sexual arousal; the other (*18*) indicated a decline in arousal as the test proceeded. We have tried a topical anesthetic (5 percent lidocaine ointment, *19*) on one additional intact male and produced, in three tests, disorientation in mounting lasting 26 to 30 minutes, after which the male achieved intromission. Full erection was observed during the period of disorientation. In three control tests with blank ointment, intromission occurred after 5 to 8 minutes. In two additional tests, when a solution of 2 percent tetracaine hydrochloride (*20*) was sprayed on the penis, disorientation and failure to achieve intromission persisted for 37 minutes when the observations were terminated. Experiments such as these are limited by the fact that anesthesia wears off during the course of the test, so that sensory feedback is delayed, not necessarily reduced. Also, the tests in rats were not continued, and a feedback process of the kind found in our cats was not detected.

In summary, long-lasting desensitization of the glans penis causes disorientation in mounting behavior which precludes intromission. This, in turn, causes further decrements in sensory feedback which leads to a pronounced seasonal decline in sexual arousal. In this last aspect our results are in agreement with Beach's theory as stated in the introduction, although the specificity of the sensory mechanism remains unanswered.

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19. Xylocaine, courtesy of Astra.
20. Cetocaine, Cetylite Industries.
21. Supported by grant HD-00348 and grant MH-08600 from NIH. Several students of the Undergraduate Research Participation program supported in part by NSF grant GE-6387 assisted in the research. We thank Miss Alba D. Plescia for technical assistance and Dr. Ethel Tobach and K. K. Cooper for reading the manuscript and for helpful suggestions.

15 February 1966

Imagery; Effect of a Concealed Stimulus

Eagle, Wolitsky, and Klein [*Science* **151**, 837 (1966)] showed subjects the black silhouette of a tree containing as part of its outline the shape of a (white) duck. Previous studies of the perception of figure and ground would lead one to expect that a subject could see either the tree-trunk or the duck at any moment in time, but not both. None of the subjects in this experiment reported seeing the duck. Nevertheless, when they were asked to close their eyes and imagine a nature scene immediately after viewing the picture, 69 percent reported duck-related items in their images, as compared with 50 percent (a small but significant difference) of the control subjects, who had been shown a similar tree without a duck outline. The authors conclude that some of the subjects were able to recognize the duck and the tree simultaneously; only one of these perceptions entered awareness, but the other was able to influence the freer activity of imaging.

An alternative explanation for this surprising result is that, when asked to close their eyes and "image," some of the subjects saw a negative afterimage of the black tree, an image consisting in part of a dark duck. Since a weak afterimage would be hard to distinguish from a spontaneous "image," it could be reported as part of the imaged nature scene even without the subject's becoming aware of its connection with the tree he had just seen. This explanation would avoid the authors' conclusion that both sides of a contour can be perceived or registered as figural simultaneously.

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3 March 1966

. . . In examining the figures of the two tree stumps, it seems to me that the figure with the duck is characterized by a "roundness," in the configuration of the extended branch and the side of the stump. On the other hand, the control figure is characterized by a roundness which is abruptly terminated, as the eye sweeps through the figure from top center, along the curved branch, to the base of the stump and then straight up. It is reasonable, I suggest, to postulate that this abrupt configuration is such as to induce less imagery of nature than the other more rounded configuration. All the responses which the authors found to be duck-related might also be found to be roundness-related. . . .

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1 March 1966

Relative Heart Weight in Porpoises

Ridgway and Johnston [*Science* **151**, 456 (1966)] compare the blood volumes, hemoglobin concentrations, packed cell volumes, and relative heart weights (percent of body weight) in three genera of porpoises. The data can be interpreted as indicating a relation between the relative heart weight (W) and the red cell volume. It might be argued that the relative heart weight is correlated with the ability to supply oxygen. This in turn is related to the red cell volume (if the heart rate, hemoglobin concentration per cell, and oxygen binding per unit of hemoglobin are approximately the same in three genera). The relationship would be of the form:

$$W = V_b \cdot V_p \cdot K, \qquad (1)$$

where V_b is the total blood volume, V_p, the packed cell volume, and K a constant. The results with Ridgway and Johnston's data are shown in Table 1, second column, the blood volume being expressed in milliliters