water where the cornea plays no role in focusing an image on the retina (*9*), the relationship between the position of the retina and the refractive strength of the lens is such that the animal will have a sharp retinal image. On the other hand, in air where the cornea makes the eye strongly myopic and astigmatic, the pupil closes down to a very narrow slit (stenopaic vision). Therefore, the refractive power of the cornea in the direction of the short axis of the slit is irrelevant since the narrow width acts as a pinhole, thus providing the eye with a huge depth of focus in that meridian. Although the optics of the cornea do play a role in the axis parallel to the length of the slit, the astigmatism in that axis combined with the spherical power of the cornea makes the eye approximately emmetropic in that meridian.

In terms of resolution of detail in moderate or good light, the underwater vision of *Zalophus* is similar to the aerial vision of the cat (*10*) and appears quite well suited for the detection and discrimination of food prey and predators as well as for the recognition of conspecific individuals or classes of individuals. The aerial vision of this species may also be used for these tasks, as well as for the recognition of landmarks for purposes of migration. These statements are intended only to upgrade the relative importance of the visual channel of these behavioral functions, and not to downgrade the acoustic channel. Each sensory modality has its own special advantages and disadvantages (*11*), and, depending upon the situation, it is likely that pinnipeds as well as other marine mammals use either the acoustic or the visual channel as a distance receptor, or use both channels by combining them in a complementary fashion.

The experiments reported here clearly show that a very vocal pinniped such as *Zalophus* has a high degree of control over its sound-production mechanism, and that its vocal behavior is susceptible to rather subtle variations in stimulus control. It appears likely that the sound emissions of some other pinnipeds as well as the odontocete whales may also be subjected to a fine degree of stimulus control, and thus may be used to determine their absolute or differential sensitivity to certain selected aspects of their environment. Therefore, psychophysical experiments may be conducted in air or under water without the use of cumbersome manipulanda normally associated with the measurement of discriminative behavior in these animals. When desired, a marine mammal may be trained to remain in a relatively fixed position for long periods of time without swimming to the manipulandum, or, on the other hand, well-placed hydrophones can pick up the controlled sound emissions of a free-swimming animal despite the relatively great distances that separate the animal and the source of the controlling stimuli.

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9. It is well known that if one does not use goggles human visual acuity suffers enormously under water. We made a preliminary test with one human subject using the same acuity targets previously presented to the sea lions. At a distance of 0.7 m the subject could quite accurately differentiate the standard target from stripes subtending a visual angle of 7.5 minutes but could not make such a discrimination when the stripes subtended a visual angle of 6.2 minutes. At distances of 4.5 and 5.5 m the subject reported that he could not even see the outline of the targets.
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l-Δ^9-trans-Tetrahydrocannabinol in Pigeons: Tolerance to the Behavioral Effects

Abstract. Δ^9*-Tetrahydrocannabinol was injected daily, in increasing doses, in pigeons under a multiple schedule of food presentation. Within a week, a dose that initially abolished responding completely was without effect. This dose was gradually increased to 20 times its original value without disrupting the behavior. No withdrawal syndrome was detected when the cannabinol was discontinued.*

Whether or not tolerance develops to marihuana and its active constituents continues to be debated. There is evidence that such tolerance develops both in animals (*1, 2*) and in man (*3*), but there is also conflicting evidence (*4*). Other evidence suggests that man can become more sensitive to some of the effects of marihuana on repeated administration rather than tolerant to these effects (*5*). Our experiments show not only that a marked tolerance develops to the behaviorial effects of an active constituent of marihuana but also that the rate, pattern, and degree of the tolerance development resembles in some respects that seen with narcotics.

In our experiments, a procedure previously employed to demonstrate behavioral tolerance to narcotics in the pigeon (*6*), was used to demonstrate the development of behavioral tolerance to *l*-Δ^9-*trans*-tetrahydrocannabinol (Δ^9THC), a constituent of marihuana, which has been shown to mimic the effects of marihuana (*7*). Two pigeons that had not received drugs previously were conditioned to peck a key for food under a multiple fixed-interval, 5-minute, fixed-ratio, 30-response (mult FI FR) schedule of food presentation (*8*). Under this schedule, in the presence of a blue key light, the 30th key peck (FR 30) resulted in a 4-second access to grain. In the presence of a red key light the first key peck after 5 minutes (FI 5) resulted in a 4-second access to grain. Key colors alternated after each presentation of grain. If the birds did not respond for 40 seconds after 5 minutes had elapsed in the presence of the red key light, the schedule changed to the FR 30 component. If the birds did not make 30 pecks within 40 seconds in the presence of the blue light, the schedule changed to the FI 5 component.

This schedule has been used to study the effects of drugs on behavior (*6, 9*). The birds were injected

Table 1. Effects of initial injections of Δ^9THC in nontolerant birds on rate of responding under the multiple schedule of food presentation. The range was determined from 9 days of Triton X 100 for birds 6512 and 1989 and from 5 days without injections for bird 6640.

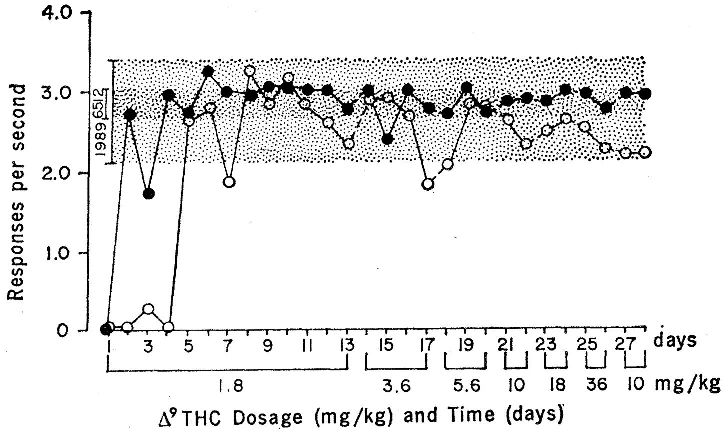
Bird	Control rate range (response/sec) FI component	Control rate range (response/sec) FR component	Δ^9THC (mg/kg)	Time after Δ^9THC (hr)	Rate (response/sec) FI	Rate (response/sec) FR
6512	1.85–2.67	2.68–3.02	1.8	2–3	0.00	0.00
				3–4	0.00	0.00
				4–5	0.03	0.09
				6–7	0.59	0.97
1989	0.57–0.89	2.12–3.43	1.8	2–3	0.00	0.00
				3–4	0.00	0.00
				4–5	0.00	0.00
				6–7	0.00	0.00
6640	1.59–2.15	3.09–3.34	5.6	2–3	0.00	0.00
				24–25	0.28	2.79
				48–49	1.24	3.00
				72–73	2.07	3.08

intramuscularly for 9 consecutive days with a 5 percent solution of Triton X 100 in distilled water at a volume of 1 ml/kg. Two hours later the pigeons were placed in sound-attenuating chambers for an hour-long session under the mult FI FR schedule. On subsequent days the pigeons were injected intramuscularly with gradually increasing daily doses of Δ^9THC suspended in 5 percent Triton X 100, and 2 hours later performance was recorded. Rates of responding during the hour-long sessions after Δ^9THC was administered were compared with the range of rates of responding when only the Triton X 100 was administered during the nine control sessions.

Table 1 shows the effects of the initial injection of Δ^9THC (1.8 mg/kg) on behavior under the mult FI FR schedule. Birds were usually tested only once daily, but since neither bird responded 2 to 3 hours after the initial Δ^9THC injections, subsequent sessions were conducted at the hours shown in Table 1. The Δ^9THC completely eliminated responding by bird 6512 during sessions 2 to 3 and 3 to 4 hours after injection. There was a gradual recovery of responding to about 30 percent of the lowest control rate, over a period of 4 to 7 hours after Δ^9THC was administered. Δ^9THC completely eliminated responding by bird 1989 during the entire period 2 to 7 hours after the first injection of 1.8 mg of Δ^9THC per kilogram of body weight.

The development of tolerance under the fixed-ratio component (FR component) of the schedule is shown in Fig. 1. Bird 6512 showed some acute tolerance to Δ^9THC on the 2nd day of injection, but bird 1989 did not. However, by the 5th day of injection of 1.8 mg/kg the rates of responding of both birds were within the control range. As the dose of Δ^9THC was gradually increased to 20 times the original dose (36 mg/kg on day 25), rates of responding under the FR component of the schedule rarely decreased below those of controls, and when decreases occurred they were slight. On the 27th day of Δ^9THC administration, a dose 20 times that which originally suppressed behavior completely had no effect on the rate of responding under the FR component.

The development of tolerance to Δ^9THC under the fixed-interval component (FI component) of the schedule is shown in Fig. 2. As occurred under the FR component, some acute tolerance was observed under the FI component in bird 6512, but not in bird 1989, on the 2nd day of Δ^9THC administration. Bird 6512 showed a more gradual development of tolerance under the FI component than under the FR component; however, tolerance developed at the same rate under both schedule components for bird 1989. By the 6th or 7th day of injection of 1.8



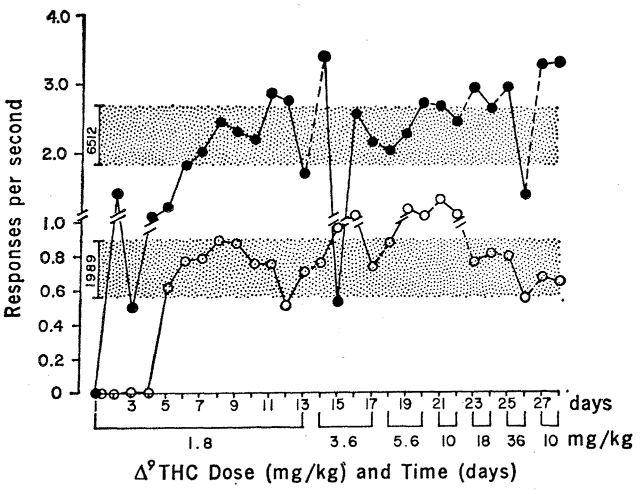


Fig. 1 (left). Effects of long-term administration of Δ^9THC on performance under the fixed-ratio component of the multiple schedule. The ordinate shows the rate of responding during a session. The abscissa shows the data for consecutive daily sessions and the dose (mg/kg) of Δ^9THC. (Open circles) Bird 1989; (closed circles) bird 6512. The shaded areas represent the range of values after nine injections of Triton X. The darker center shading is the range for bird 6512 and the wider, lighter shading is the range for bird 1989. Fig. 2 (right). Effects of long-term administration of Δ^9THC on performance under the fixed-interval component of the multiple schedule. The ordinate shows the rate of responding during a session. The abscissa shows consecutive daily sessions and dose (mg/kg) of Δ^9THC. (Open circles) Bird 1989; (closed circles) bird 6512. The upper shaded area represents the range of values after nine injections of Triton X for bird 6512 and the lower shaded area is the same range for bird 1989.

mg/kg, the rates of responding under the FI component were within the control range. During subsequent sessions, as the dose was increased to 20 times the original dose, rates of responding fell below those of controls infrequently. During some sessions, however, administration of Δ^9THC did increase the rates of responding relative to the control rates of responding after Triton X 100. Similar rate increases during the FI component of a mult FI FR schedule have been observed after daily injections of morphine and methadone in pigeons (*6*), but rate increases have not been observed with pigeons for Δ^9THC when injections were widely spaced during the determination of dose-effect curves (*2*), although rate-increasing effects of tetrahydrocannabinols also have been observed in monkeys when shock-avoidance procedures were used (*10*).

Doses of Δ^9THC of 10 mg/kg or higher were given for 8 days after the 28 days shown in Figs. 1 and 2, and then administration was discontinued. Although small changes in the rates of responding were observed when the drug was withdrawn, no gross behavioral symptoms suggesting a withdrawal syndrome could be detected, nor did the general health of the pigeons seem to be impaired during or after long-term administration. Bird 6512 was given 10 mg/kg (from the same sample of Δ^9THC used previously) after 4 weeks during which no injections were given. Much of the tolerance to this dose had disappeared during the 4-week period, since bird 6512 responded at a rate of 0.07 response per second during the FI component and at a rate of 0.18 response per second during the FR component.

During the course of these experiments, the purity of the Δ^9THC was established both by gas chromatography and by injections of the solutions used into birds (6640 and 5117) that had not previously received Δ^9THC. Table 1 shows the effects of 5.6 mg/kg in bird 6640. The injection was drawn from the same sample used to inject the two pigeons in the tolerance study. The table shows that the 5.6 mg/kg dose, which did not decrease responding under either schedule component in the tolerant birds, completely eliminated the responding of bird 6640 2 hours after injection, and effects could still be seen 48 hours after injection. In another experiment, a dose of 36 mg/kg was given to bird 5117. Within 2 hours this bird could not stand, walk, or fly normally and refused food. At 8 hours after the injection, the bird lay on the cage floor with labored respiration. The bird did not stand up until 48 hours after the injection, and he did not eat until 72 hours after the injection. Yet this dose (36 mg/kg) had no effect on schedule-controlled behavior in the tolerant birds.

Our experiments demonstrated that a dose of Δ^9THC which completely disrupts food-reinforced responding in pigeons for many hours can be increased more than 20-fold without disrupting this schedule-controlled behavior in tolerant birds. Since no behavioral effect was obtained at this very large dose, the 20-fold increase probably does not represent the limits to which tolerance to Δ^9THC can develop. The degree of behavioral tolerance we obtained in these pigeons is more like that reported for morphine in animals (*11*) than like the lesser degree of tolerance which develops to the barbiturates in animals and man (*12*). The pattern of the development of tolerance to Δ^9THC is similar to that seen with morphine and methadone in similar behavioral experiments with pigeons (*6*), both in the rate of the development of tolerance under the FI component and in the appearance of rate-increasing effects during long-term administration.

Previous failures to demonstrate development of tolerance to the effects of marihuana in man and animals (*4, 5*) may have been related to the route of administration, the purity of the drug preparation, or to the species. Although our data do not determine the relative importance of each of these variables, and therefore limit any generalization of our results to man, they do indicate that a tolerance resembling somewhat that seen with narcotics, can develop in pigeons when Δ^9THC is given parenterally at high doses.

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Many Responses per Food Reward with Free Food Present

Carder and Berkowitz (*1*) showed that, when ten lever presses were required to produce one pellet of food, rats ate freely available pellets almost exclusively and rarely pressed the lever. They also confirmed Jensen's (*2*) original finding that when each press was immediately reinforced with a pellet, rats frequently pressed a lever although free pellets were continuously available. In an extension of work previously reported (*3*), I found that pigeons behaved in essentially the same way. With free grain present, pigeons responded to a disk if the fixed ratio of responses to grain reinforcements was less than 5 : 1 but did not respond significantly if the ratio was greater than 10 : 1.

Under a different procedure, however, the pigeons pecked a disk more than 40 times for each food reinforcement while free identical food was available. Three male White Carneaux pigeons, with previous experiences in a variety of operant-conditioning experiments, were maintained at 80 percent of their normal weights. The subjects received 15 preliminary sessions on a 1-minute variable-interval schedule of reinforcement. On the average of