treme, but not uncommon situation, small trees or trees supporting multiple colonies are completely denuded. In the latter case colonies are occasionally able to establish trails over the ground to distant trees. Increased foraging efficiency and inclusive fitness resulting from the sharing of successful search efforts among siblings may well have been a major impetus for the evolution of aggregative behavior in this species.

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References and Notes

1. T. D. Fitzgerald and E. M. Gallagher, *J. Chem. Ecol.* **2**, 187 (1976).
2. E. O. Wilson, *The Insect Societies* (Belknap, Cambridge, Mass., 1971).
3. This was determined by placing a fine thread in the path of a larva, then lifting it after it had passed. Of 480 larvae (eight colonies) moving from the tent to feeding sites over previously silked trails, 94 percent were spinning. Only 13 percent of these same larvae added silk to the trail as they returned to the tent after feeding. Larvae crossing previously unsilked branches, however, usually spun silk on both the outbound and return trip. Returning larvae rarely continued to spin after reaching the tent or the heavily silked bridge.
4. The silk was obtained by letting small groups of larvae that had not fed for more than 6 hours circle in petri dishes.
5. A separate test was conducted to determine if the choice of larvae in this and other tests recorded in Table 2 was also influenced by the choice of preceding larvae, since each outbound forager reinforced the trail with an additional strand of silk. The first 15 caterpillars let out onto the fork following the return of the initial contingent of 30 were channeled onto the arm crossed by the unfed returning larvae. The choice of larvae in the next group of 15 was then recorded. An average of 92 percent of these larvae (five tests) still selected the trail used by the fed, returning larvae. However, when the trails formed by the initial contingent of 30 larvae were allowed to age for 6 hours before the additional larvae were channeled onto the arm used by the unfed returning larvae, the additional silk deposited by these caterpillars had a marked influence on the choice of the next 15 caterpillars. An average of 46 percent of these larvae (five tests) selected the trail reinforced with the new silk.
6. I want to thank A. Costanzo for his technical assistance.

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A Blind Fish Can School

Abstract. *Vision is not required in order for fish to school. Five individual saithe,* Pollachius virens, *were able to join schools of 25 normal saithe swimming in an annular tank, while blinded with opaque eye covers. Test fish maintained position within the school indefinitely and responded to short-term movements of individuals within the school, although quantitative differences in reaction time and schooling behavior were noted. Five fish with lateral lines cut at the opercula were unable to school when wearing opaque eye covers. Although it is unlikely that blind saithe could school in the wild, the constraints of the apparatus permitted a demonstration of a role of the lateral line organ in schooling.*

Vision has long been considered a vital sensory component of schooling behavior (*1–3*) not least because fish usually stop schooling at low light intensities (*4*). Individual blind fish sometimes turned toward normal members of their own species (*1–3, 5, 6*) and have occasionally been observed to swim parallel to a control school for a few seconds (*3*) but have never been observed to maintain position for longer. We report here that adult saithe, *Pollachius virens*, wearing opaque eye covers (blinders) were capable of maintaining position indefinitely in a school of normal saithe swimming at approximately two body lengths per second, although their behavior within the school was quantitatively different from that of normal fish.

Underwater motion pictures taken in the wild (C.S.W.) show that saithe swim in polarized and synchronized groups, thus meeting Shaw's (*3*) definition of schooling. The film suggests that saithe are one of the strongest facultative schoolers (*7*) among the gadoid fishes.

Twenty-five newly caught saithe between 25 and 35 cm long were individually freeze-branded and introduced into an annular channel 1.5 m wide in the 10-m diameter gantry tank at the Marine Laboratory, Aberdeen, Scotland. A rectangular pool of light was projected onto the floor of the annular channel from spotlights on the counterclockwise rotating radial gantry; superimposed on it was a random speckled light pattern. The school of saithe were trained during a period of 4 days to swim above this moving background and, thereby, to remain in roughly the same area relative to the gantry (*8*). A continuous record of fish schooling in this area was provided in plan view by a television camera mounted on the gantry and linked to a videotape recorder. A saithe from the trained school was anesthetized and fitted with opaque blinders, which completely covered both eyes. After the fish had partially recovered from the anesthetic, it was returned to the channel, where it soon swam slowly about in a restricted area. (The rest of the school was swimming continuously around the tank.) The fish with blinders avoided swimming into the walls of the channel (*5*). After about an hour it began to respond to the school, turning toward the leading fish as they passed on each circuit of approximately 69 seconds. The test fish soon began to follow and then swim with the school for increasing distances, until after about 3 hours, it was able to school indefinitely (Fig. 1). After experiments lasting an additional 3 to 4 hours, we caught the test fish, removed the eye covers, and returned it to the tank, where it immediately rejoined its fellows and behaved quite normally. Three more fish tested in the same manner were each found capable of schooling while effectively blind.

In order to be certain that these fish were unable to see, we fitted blinders lined with a smooth layer of aluminum foil to another test fish. This saithe took longer to begin schooling again (about 6 hours), but once it had started, its behavior in the school was similar to that seen in the other four blind fish experiments. Further evidence that all the test fish were unable to see objects is that although hand-netting normal saithe from the channel was very difficult, none of the temporarily blinded fish avoided the mouth of nets placed in their path, even in bright light. In addition, the test saithe soon became dark in color (Fig. 1); this response is typical of blind fish, who match their skin color to their visual assessment of the surroundings (*9*).

When the school was startled by one of the experimenters suddenly reaching over the side of the tank, blind fish responded only if their neighbors were less than one body length away (Fig. 2) and only after these adjacent fish had accelerated. For six cases in which the fish with blinders did startle, the average lag from the acceleration of their nearest neighbor was 0.4 second (20 frames on the video record). The average lag for normal fish was 0.045, but this value is not strictly comparable since sighted fish may have responded directly to the stimulus (*10*). When startled, blinded fish tended to bump into the walls of the tank and into other fish, whereas sighted fish rarely did this. On no occasion did we observe a test fish collide with the walls of the tank or other objects when approaching them at normal speed. Very occasionally they swam into others in the school, but only when the latter were executing some rapid maneuver [see also (*5*)].

Fish wearing blinders did not school normally but appeared to change position within the school far more often than their sighted fellows did. In order to test this, we superimposed a square grid on the video image and recorded the frequency with which test fish and controls

Fig. 1 (left). The blind fish (arrow), appearing darker than its fellows, is almost in the center of the school in this photograph of a single video frame. The eye covers, which are just visible, were made of overexposed photographic film further blackened with waterproof marker and lined with aluminum foil. Although the random pattern of projected light spots has been turned off, the fish are continuing to school. The orientation of the blind fish is slightly different from that of the rest of the school as it lags behind in a turn. The distance between the images of each fish and its shadow is used to calculate the height of each fish in the water (*17*). Fig. 2 (right). Photograph of a single frame from videotape. Members of the school are seen responding to the experimenter's hands appearing over the side of the tank (upper left) but the blind fish (arrow) is not responding. The speckled light pattern that the fish followed around the tank is visible.

crossed the grid lines. Since the camera was moving at the same speed as the school, most fish remained fairly stationary within the video image so that (for our camera orientation) the frequency with which a fish crossed horizontal and vertical lines of our grid gave measures of, respectively, side-to-side and fore-and-aft motion within the school. For each of the five blind fish experiments, five sequences of behavior were analyzed frame by frame on the videotape ($\bar{X} = 15.5$ seconds, at 50 frames per second). Test fish crossed horizontal grid lines more than four times as often as randomly selected control fish from the school (Wilcoxon one-tailed test, $P < .01$). This difference resulted partly from a tendency of the temporarily blind fish to swim straight ahead, tangentially to the circular track, while fish in the accompanying school must have made a series of small turns to steer an apparently smooth circumferential course in the channel. Course corrections by blind fish were made less frequently and were of greater magnitude. They also showed greater latencies than their sighted neighbors in responding to changes in velocity of fish in the school, both for minor accelerations and in the startle experiments.

The quantitative differences in schooling were not caused by irritation produced by the blinders, since fish wearing blinders with a hole cut out for the pupil or clear eye covers schooled immediately when they were reintroduced into the tank and did not show the same degree of lateral displacements as the fully blind saithe. Several potential test fish whose blinders fell out schooled normally immediately thereafter; they therefore control for the effects of the fitting operation.

In order for a blind fish to school it must (i) locate and join a moving group of fish and (ii) respond to short-term movements and changes in velocity of individuals within it. A blind fish might be able to do the first and not the second if, for example, it merely responded to the sound of the motor driving the gantry or to the light to dark boundary of the moving pool of light by way of the pineal body. This was not the case since, on the few occasions when the control school was absent from the spotlit area (so that only sound and light cues were present), test fish failed to turn and swim with the moving boundary. In contrast, the videotapes show a number of instances in which turns were an unequivocal response to the leading fish of the school (*11*).

We have no evidence that sound, light, or olfactory cues could account for the observed adjustments in position and velocity of the blind fish, once they had joined the school. For example, pattern recognition necessary for responding to other fish in the school could not occur by way of the lensless, unorganized mass of photoreceptors in the teleost pineal body (*1, 2, 12*). There are reports that bioelectric fields can be detected by teleosts with no special electro-receptors (*13*). Although such sensory receptors might account for the schooling of our test fish, they could not account for the ability of isolated blind saithe to avoid inanimate objects in the tank.

We believe that the sensory input used by blinded fish to maintain position within the moving school is the lateral line organ. Experiments on tuna separated by transparent barriers have indicated that the lateral line organ plays a role in the maintaining interfish spacing (*14*). We were unable to induce schooling in five blind saithe in which the lateral lines were cut at the operculum. However, five saithe with lateral lines cut, but with normal vision, showed apparently normal schooling (*15*); thus, lateral line information, like vision, is not necessary for schooling to take place.

Like the blind fish, the fish with blinkers and lateral line cuts could respond to bright light, probably by way of the pineal body. Although three of the five fish with lateral line cuts refused to swim at all while wearing blinkers, two could be induced to swim around the tank in front of a pole hanging from the moving gantry. Even when they were "poled" into the school, however, they did not respond to movements of neighbors, and, if the pole was removed from the water, they immediately fell back out of the school and stopped swimming.

Two previous studies have failed to demonstrate schooling in temporarily blinded fish. When Keenleyside (*1*) fitted small rudd, *Scardinius eryopthalmus*, with aluminum foil blinkers, three blind fish would not school with three sighted fish. A single blind saithe probably had a much greater opportunity and motivation to school than Keenleyside's rudd since (i) it had been trained previously to swim around the tank, (ii) the school met the test fish once a minute at each circuit of the tank, and (iii) one test saithe had 25 normal schooling fish to respond to. If we allow for the different experimental procedures, Keenleyside's findings do not seem incompatible with our own. Parr (2) found that seven chub mackerel, *Scomber colias*, temporarily blinded with a mixture of lamp black and Vaseline applied to both eyes, failed to join a milling school of normal fish and collided repeatedly with them.

We do not know whether the differences between our results and those of Parr are consequences of technique or whether they reflect real differences between the two species; the extent of arousal may also be important. Parr's fish showed panic reactions which increased the more they collided, whereas the test saithe recovered very gradually from handling and anesthesia while being repeatedly presented with the school. Finally, none of our blind saithe showed any reaction to the school within the time scale of Parr's experiment. It is therefore likely that the present technique allows more chance for a blind fish to school.

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References and Notes

1. M. H. A. Keenleyside, *Behaviour* **8**, 183 (1955).
2. A. E. Parr, *Occas. Pap. Bingham Oceanogr. Coll.* **1** (1927); A. Schaifer, *Zoologica* **27**, 75 (1942).
3. E. Shaw, in *The Development and Evolution of Behavior*, L. R. Aronson *et al.*, Eds. (Freeman, San Francisco, 1970), p. 452.
4. J. R. Hunter, *J. Fish. Res. Board Can.* **25**, 393 (1968).
5. E. S. Bowen, *Ecol. Monogr.* **1**, 1 (1931).
6. K. R. John, *Copeia* **2**, 123 (1957).
7. B. K. Noble and B. Curtis. *Bull. Am. Mus. Nat. Hist.* **76**, 1 (1939).
8. C. M. Breder, *Zoologica* **52**, 25 (1967).
9. C. S. Wardle and P. D. Anthony, *Int. Counc. Explor. Sea. Coop. Res. Rep. Ser. B* **22** (1973).
10. P. Rasquin, *Bull. Am. Mus. Nat. His.* **115**, 1 (1958).
11. See also J. R. Hunter, *Anim. Behav.* **17**, 507 (1969).
12. During 3.5 hours of videotaping, there were no occasions in which a test fish appeared to adjust its position to a light speckle; on many occasions it responded to another fish changing position within the school. An olfactory cue is unlikely as well. To give information accurate to 1 meter, any pheromone would have to decay detectably in less than 2.5 seconds since a revolution took 69 seconds.
13. P. R. T. Pary, *Am. Zool.* **5**, 682 (1965); E. Dodt, *Experientia* **19**, 642 (1963).
14. V. R. Protasov, B. M. Basov, V. I. Krumin, A. A. Orlov, *Zool. Zh.* **49** (5) (1970), cited by D. V. Radakov, *Schooling in the Ecology of Fish*, H. Mills, Trans. (Wiley for Israel Program for Scientific Translations, New York, 1973); R. C. Peters and T. van Wijland, *J. Comp. Physiol.* **92**, 273 (1974); Ad. J. Kalmijn, in *Handbook of Sensory Physiology*, A. Fessard Ed. (Springer-Verlag, Berlin, 1974), vol. 3, p. 147; E. Schwartz and A. D. Hasler, *Z. Vgl. Physiol.* **53**, 317 (1966). Experimental evidence that bioelectric fields are used in orientation has come from catfish, which have specialized electro-receptor pits, whereas gadoids do not have this type of pit.
15. P. H. Cahn, *Lateral Line Detectors* (Indiana Univ. Press, Bloomington, 1967); *U.S. Fish. Wildl. Serv. Fish. Bull.* **70**, 197 (1972).
16. There may be quantitative differences in spacing and velocity adjustment. A full analysis of the exact three-dimensional position of saithe in these experiments is in progress.
17. J. M. Cullen, E. Shaw, H. A. Baldwin, *Anim. Behav.* **13**, 534 (1965).
18. We thank the Marine Laboratory, of the Department of Agriculture and Fisheries, Aberdeen, Scotland, for the use of the gantry tank and ancillary facilities and R. S. Batty and W. Mojsiewicz for practical help. J. M. Cullen, A. Macfadyen, R. Dawkins, and A. Cook criticized the manuscript. This work was supported in part by a New University of Ulster research grant to T.J.P.

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Cannabinoid Induced Behavioral Convulsions in Rabbits

Abstract. *A population of New Zealand White rabbits has been found to exhibit behavioral convulsions when given low intravenous doses of psychoactive cannabinoids of marijuana. The behavioral convulsions decrease in severity and then disappear after the long-term administration of Δ^9-tetrahydrocannabinol. The extreme sensitivity of these rabbits to the stimulant action of cannabinoids suggests that the population might serve as a model in studies of the stimulant action of cannabinoids.*

Although the anticonvulsant properties of Δ^9-tetrahydrocannabinol (Δ^9THC) have been well established in experimental animals (*1*) there is some evidence that this major psychoactive component of marijuana possesses convulsant properties. Electroencephalographic (EEG) patterns of convulsive-like activity, for example, polyspikes, spike and slow waves, have been reported in rodents, dogs, cats, rabbits, and monkeys, but these EEG manifestations occur in the absence of behavioral convulsions (*1*). While behavioral convulsions occasionally have been reported in rats, dogs, and monkeys, these seizures generally occur only with lethal or near-lethal doses of Δ^9THC (*1*).

Recently, we have found that some rabbits of the New Zealand White breed exhibit behavioral convulsions when given an intravenous dose of Δ^9THC as low as 0.05 mg per kilogram of body weight (*1–3*). These rabbits were subsequently inbred and the resultant offspring were tested with additional naturally occurring and synthetic cannabinoids of marijuana. Here, we describe the behavioral effects of various cannabinoids in these rabbits, and demonstrate that the behavioral convulsions decrease in severity after the long-term administration of Δ^9THC.

The lineage of this population of New Zealand White rabbits is shown in Fig. 1. The first four rabbits found to be susceptible to convulsions induced by Δ^9THC were Nos. 20, 21, 22, and 24 (*2*). The parents of this litter were tested and the dam was found to be seizure susceptible while the sire was not. Among the litters bred from this single pair of rabbits, about 90 percent of the individuals exhibit convulsions after the intravenous administration of Δ^9THC in doses of 0.5 mg/kg or less. The seizures induced by Δ^9THC are apparently due to an autosomal recessive mutation in the rabbits, similar to that found in rabbits that are susceptible to audiogenic seizures (*4*), but in the New Zealand White population it is the high degree of penetrance that confers susceptibility to Δ^9THC. Standard genetic tests are being made to define clearly the mode of inheritance.

In the present experiments, the rabbits used ranged in weight from 2.5 to 3.3 kg. A catheter was implanted in the left external jugular vein so that drugs could be administered intravenously without disrupting the animal's behavior during subsequent testing. Surgery was performed with the animals under chlorpromazine and subsequently pentobarbital anesthesia. All cannabinoids except 4-morpholino-butyrate-Δ^9-THC (SP-111A) were prepared in a vehicle of 10 percent polysorbate (Tween 81) and saline. Since SP-111A is water soluble, distilled water was used as the vehicle for this synthetic derivative of Δ^9THC.

During testing, subjects were observed through a one-way vision window in a sound attenuated chamber measuring 82 cm square by 70 cm high. As previously described (*2*), the frequency and duration of the following behaviors were measured by an experimenter-operated digital event recorder: limb clonus; extension of front or hind limbs, or both; head tuck; body torsion; ears down; mydriasis; and nystagmus. Latency to convulsion (that is, the first onset of clonus or tonus, or both) was also mea-