stretching suggests the absence of secondary spindle input (Fig. 2C). Of 36 force-sensitive interneurons, 31 did not respond under these conditions. In the remaining 68 force-sensitive interneurons, stretching excited the interneuron but also produced significant passive muscle force (Fig. 2D). Since increases in muscle force excite unidentified mechanoreceptors and since most of the force-sensitive interneurons were strongly influenced by unidentified mechanoreceptors, the response at long muscle lengths (Fig. 2D) may be due to input from unidentified mechanoreceptors rather than secondary spindle afferents.

To the best of our knowledge, no previous descriptions of spinal neurons that respond to increases in muscle force have been published. Except for a single early study (*9*), preceding investigations of proprioceptive spinal reflexes based on recordings from spinal interneurons have been concerned with connectivity (*10*) and cellular properties (*11*). Although we anticipated that force dependence would be due to Golgi tendon organ input, our finding that unidentified mechanoreceptors potently excite force-sensitive interneurons, together with the results of others showing that group III and IV afferents are excited by increases in muscle force (*12*), indicate that unidentified mechanoreceptors may be at least partly responsible for the force dependence of force-sensitive interneurons. This conclusion is supported by our finding that only 10 of 39 force-sensitive interneurons could be shown to receive electrically induced Ib afferent input.

The response patterns of force-sensitive interneurons are unlike those required for simple force feedback. The discharge of interneurons mediating simple force feedback might be expected to be influenced significantly only by input from Golgi tendon organs, to vary linearly with static muscle force, and to exhibit a time course of discharge closely paralleling muscle force. Instead, we found that force-sensitive interneurons are influenced by unidentified mechanoreceptors [some of which can be excited by muscle stretching and mechanical pressure as well as by muscle force (*12*)] and usually show nonlinear force-rate relations. Finally, the early, transient overshoot in discharge rate and prolonged afterdischarge are also inconsistent with simple force feedback. In contrast, the clasp knife reflex has properties similar to those of force-sensitive interneurons. Muscle stretching excites force-sensitive interneurons and induces the clasp knife reflex only at long muscle lengths. At short lengths, neither motoneurons nor force-sensitive interneurons are influenced. The sustained afterdischarge of force-sensitive interneurons is matched by the sustained inhibition of the clasp knife reflex. Finally, lightly stroking the muscle surface, which potently excites force-sensitive interneurons also produces an abrupt and prolonged inhibition of motoneuronal output. Therefore, provided force-sensitive interneurons inhibit homonymous motoneurons, these interneurons most likely mediate the clasp knife reflex. Although the clasp knife reflex has only been demonstrated in decerebrated cats with dorsally hemisectioned spinal cords and in spastic human patients, the central pathways responsible may still influence motoneurons under normal conditions.

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References and Notes

1. P. E. Crago, J. C. Houk, W. Z. Rymer, *J. Neurophysiol.*, in press.
2. Y. LaPorte and D. P. C. Lloyd, *Am. J. Physiol.* **169**, 609 (1952); J. C. Eccles, R. M. Eccles, A. Lundberg, *J. Physiol. (London)* **138**, 227 (1957).
3. J. C. Houk, J. J. Singer, M. R. Goldman, *J. Neurophysiol.* **33**, 784 (1970); J. J. B. Jack and R. C. Roberts, *J. Physiol. (London)* **305**, 42P (1980); W. Z. Rymer and Z. Hasan, *Brain Res.* **184**, 203 (1980); J. A. Hoffer and S. Andreassen, in *Muscle Receptors and Movement*, A. Taylor and A. Prochazka, Eds. (Oxford Univ. Press, New York, 1981), p. 311.
4. R. M. Eccles and A. Lundberg, *J. Physiol. (London)* **147**, 565 (1959).
5. W. Z. Rymer, J. C. Houk, P. E. Crago, *Exp. Brain Res.* **37**, 93 (1979); D. Burke, L. Knowles, C. Andrews, P. Ashby, *Brain* **95**, 31 (1972).
6. J. J. B. Jack, in *Studies in Neurophysiology*, R. Porter, Ed. (Cambridge Univ. Press, New York, 1978), p. 155.
7. P. B. C. Matthews, *Muscle Receptors* (Arnold, London, 1972), pp. 1–8.
8. M. C. Brown, I. Engberg, P. B. C. Matthews, *J. Physiol. (London)* **192**, 773 (1967).
9. G. M. Kolmodin, *Acta Physiol. Scand. Suppl.* **139**, 1 (1957).
10. J. C. Eccles, R. M. Eccles, A. Lundberg, *J. Physiol. (London)* **154**, 89 (1960); M. Lucas and W. D. Willis, *J. Neurophysiol.* **37**, 282 (1974); E. Jankowska, T. Johannisson, J. Lipski, *J. Physiol. (London)* **310**, 381 (1981).
11. L. Haapanen, G. M. Kolmodin, C. R. Skoglund, *Acta Physiol. Scand.* **43**, 315 (1958); C. C. Hunt and M. Kuno, *J. Physiol. (London)* **147**, 346 (1959).
12. A. S. Paintal, *ibid.* **152**, 250 (1960); M. Franz and S. Mense, *Brain Res.* **92**, 369 (1975); K.-D. Kniffki, S. Mense, R. F. Schmidt, *Exp. Brain Res.* **31**, 511 (1978).
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Spatial Learning as an Adaptation in Hummingbirds

Abstract. *An ecological approach based on food distribution suggests that hummingbirds should more easily learn to visit a flower in a new location than to learn to return to a flower in a position just visited, for a food reward. Experimental results support this hypothesis as well as the general view that differences in learning within and among species represent adaptations.*

Learning is a mechanism by which animals modify their behavior to respond more efficiently to their environments. Like other adaptations, learning has evolved as the result of the interactions that occur between animals and their environments. From this perspective, the characteristics of learning should vary because the ecological and social conditions in which animals learn are varied. With sufficient information on the ecology of animals it should be possible to make a priori predictions about learning. We tested predictions about the ability of hummingbirds to learn different spatial patterns of food availability from individual flowers.

Hummingbirds obtain most of their energy from floral nectar, present in individual flowers in small, slowly renewed amounts (*1*). The small size of hummingbirds and their hovering flight while feeding make them dependent on short-term supplies of energy, requiring visits to many flowers (*2*). Their foraging efficiency depends on the difference between the rates of gain and expenditure of energy. Several experiments indicate that animals often approach maximum rates of net energy gain when they feed (*3*). Although learning may enhance energy returns, only a few experiments have examined the impact of learning (*4*).

In their natural environment, hummingbirds returning to a recently emptied flower would have a lower rate of net energy gain than birds going to a flower that contains nectar. We hypothesized that a hummingbird reinforced for visiting a flower location should more easily learn to choose a different location during a subsequent foraging effort than learn to return to the same location.

We studied four female *Archilochus alexandri* (black-chinned hummingbird; 3 to 4 g), two male *Eugenes fulgens* (Rivoli's hummingbird; 8 to 10 g), and two male *Lampornis clemenciae* (blue-throated hummingbird; 8 to 9 g) captured wild in southeastern Arizona (*5*). They were maintained individually in 1-m^3

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Table 1. Trials and errors to criterion and first-day performance of each hummingbird during shift and stay learning; S.E., standard error.

Hummingbird	Shift learning				Stay learning			
	Trials to criterion	Errors to criterion	Percentage correct, day 1	Learning rate to criterion (percent/day)	Trials to criterion	Errors to criterion	Percentage correct, day 1	Learning rate to criterion (percent/day)
				Stay first				
Archilochus 1	160	82	20	6.7	640	239	40	1.2
Archilochus 2	180	96	25	6.5	620	238	35	1.4
Eugenes 1	96	42	38	11.6	282	130	29	4.9
Lampornis 1	144	43	50	5.4	624	273	50	1.5
Mean ± S.E.	145 ± 17.9	65.7 ± 13.7	33.2 ± 6.8	7.6 ± 1.4	441.5 ± 104.5	220 ± 31.0	38.5 ± 4.4	2.2 ± 0.9
				Shift first				
Archilochus 3	200	48	60	1.8	1240	506	40	0.9
Archilochus 4	80	25	70	2.0	360	138	30	2.6
Eugenes 2	24	5	79	4.0	360	149	25	4.5
Lampornis 2	96	24	67	5.2	790*	341*	35	2.8
Mean ± S.E.	100 ± 36.7	25.5 ± 8.8	69.0 ± 3.9	3.2 ± 0.8	687.5 ± 210.2	283.5 ± 87.6	32.5 ± 3.2	2.7 ± 0.7

*Did not reach criterion; this represents a minimum estimate.

cages in an aviary with temperature controlled at 24° ± 2°C and with a photoperiod of 14 hours of light and 10 hours of darkness. The maintenance food was *Drosophila* and a 0.5*M* sucrose solution with vitamins, minerals, and amino acids (*6*). The birds maintained in this manner have remained healthy for more than a year and have completed at least one molt.

Birds were deprived of food for 1/2 hour before the testing period each day. They were placed in a 1-m^3 cage with a perch. A 0.5*M* sucrose solution was provided in "flowers" made from yellow plastic syringe needles plugged with clay and fitted with a plastic corolla that extended 12 mm from the top of the syringe needle cap (*7*). Flowers could be presented at two locations, 12.5 cm to the right or left of the middle of a Styrofoam strip placed against the side of the cage opposite to the perched bird.

During the initial (information) stage of each trial, a single flower containing food was presented. The position of this flower varied randomly from trial to trial, except that the position was never the same for more than three consecutive trials. After the bird was fed, the strip was removed and the second (choice) stage of the trial was begun within 10 to 12 seconds. Two flowers were presented, one containing food and the other empty. The hummingbird was allowed to visit only one flower. A visit was defined as a bird inserting its bill into the corolla. If a correct response was made, the bird consumed the food, and the flowers were removed. If an incorrect response was made, the flowers were withdrawn immediately. In either case, the next trial was begun 3 minutes later. The *Eugenes* and *Lampornis* were given 24 trials per day and the *Archilochus* were given 20 trials per day for 5 days per week.

Two problems were presented. "Stay learning" required a return to the position that had been visited during the information stage of the trial in order to obtain a reward during the choice stage. "Shift learning" required going to the opposite position to obtain food. All birds were trained on both tasks. Four birds first learned stay and then shift, while the other four birds learned the tasks in reverse order (Table 1). Training on each task continued until at least 80 percent of the choices were correct each day for three consecutive days.

Every hummingbird learned the shift task in a shorter time than it learned the stay task, regardless of the order of presentation of the two tasks (Table 1). The slowest shift learning by any bird (*Archilochus* 2, 180 trials and 96 errors) was much more rapid than the fastest stay learning by any bird (*Eugenes* 1, 282 trials and 130 errors). These differences between stay and shift learning were statistically significant for both groups (Wilcoxon matched pairs test, $T = 0$, $P < .01$).

Two factors contributed to the more rapid achievement of criterion during shift learning: (i) different levels of shift and stay performance at the start of training and (ii) different rates of improvement on the two tasks. That the hummingbirds had a preexperimental bias toward shift behavior was evident during the first day of the experiment. They shifted about two times as often as they stayed, regardless of the task. Thus the birds being trained to shift were more often correct than those being trained to stay, on the first trial day (Table 1; Mann-Whitney $U = 0$; $P < .05$).

An initial bias toward shifting, however, does not in itself account for the results. The average daily improvement (percentage improvement per day; Table 1) for each bird was significantly higher during shift learning than during stay learning ($T = 3$, $P < .05$). This higher rate of shift learning also can be seen by comparing stay and shift learning when each was the second task to be learned. The birds showed virtually identical percentages of correct responses during the first day ($U = 7$; $P > .40$) because of previous training, but the shift task still was learned more rapidly ($U = 0$; $P < .05$).

The differences in learning rates were notable in view of the similarity in the structure of stay and shift tasks. In each case, the only cue for location of nectar was the location of the flower that had just been visited, and in each case, the correct response was a visit to a specific location. The only difference between the tasks was the rule used to relate the correct location to the remembered location. Therefore, the reason for the differences in learning rates must be sought in something other than the structure of the tasks. Similar learning occurs in rats using position cues (*9*), and the ease of shift learning is not predicted by the traditional views of the effects of reinforcement on behavior (*10*).

These results support the hypothesis that spatial learning in hummingbirds is related to the spatial distribution of resources influencing rates of net energy gain. The preexperimental bias toward shift behavior of these wild-caught birds may have been innate or may have reflected their earlier field experiences. But the differences in learning rates, especially during the second stage of the experiment, are unlikely to represent these kinds of effects. It is possible that an evolved tendency for hummingbirds to shift locations of flower visits is manifested in starting performance as well as in differential rates of learning. For non-

spatial cues, such as colors, sounds, and shapes, stay learning should be more rapid than shift learning. This difference may be due to the nature of position as a cue, for each position in space is unique.

Differences between and within species in the ease of shift and stay learning may depend on the influence of the spatial and temporal scale of resource depletion after feeding. Shift learning should occur whenever the positions are divided so finely that visits always produce depletion; stay learning should occur whenever visits do not result in appreciable resource depletion. In hummingbirds, for example, stay learning may occur more easily at patches of inflorescences. Temporal scales may also be important for resources that are renewed, since the rate of renewal should determine the value of a site for future visits.

An ecological approach to learning, based on an analysis of the problems animals face in their natural environments, can generate useful predictions about differences in learning between and within species. This is in contrast to the recent approach called biological "constraints" on learning (*11*), which requires the analysis of apparent anomalies in arbitrary learning situations. Our results suggest that the ecology of food resource distribution in space and time generates important evolutionary influences on learning.

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References and Notes

1. L. L. Wolf, F. G. Stiles, F. R. Hainsworth, *J. Anim. Ecol.* **45**, 349 (1976); H. G. Baker, *Biotropica* **7**, 137 (1975); A. Kodric-Brown and J. H. Brown, *Ecology* **49**, 285 (1978).
2. C. A. Beuchat, S. B. Chaplin, M. L. Morton, *Physiol. Zool.* **52**, 280 (1976); C. L. Gass, *Can. J. Zool.* **56**, 1535 (1978); F. R. Hainsworth and L. L. Wolf, *J. Comp. Physiol.* **80**, 377 (1972).
3. For reviews see C. L. Gass and R. D. Montgomerie, in *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*, A. C. Kamil and T. D. Sargent, Eds. (Garland, New York, 1981), pp. 159–194; J. R. Krebs, in *Behavioural Ecology*, J. R. Krebs and N. B. Davies, Eds. (Sinauer, Sunderland, Mass., 1978), pp. 23–63.
4. B. Heinrich, P. R. Mudge, P. G. Deringis, *Behav. Ecol. Sociobiol.* **2**, 247 (1977); A. C. Kamil, *J. Comp. Physiol. Psychol.* **92**, 388 (1978); T. M. Laverty, *Can. J. Zool.* **48**, 1324 (1980); J. N. M. Smith and H. P. A. Sweatman, *Ecology* **55**, 1216 (1974).
5. The Department of Interior Fish and Wildlife Service, the Arizona Department of Fish and Game, and the New York State Department of Conservation provided the necessary permits.
6. Nutritional components were provided by K.-L. Schuchmann [see K.-L Schuchmann, *Kolibris: Haltung, und Pflege* (Biotropic Verlag, Frankfurt, 1979)].
7. The *Archilochus* obtained 30 μl per rewarded flower while the *Lampornis* and *Eugenes* obtained 20 μl per flower. These amounts are much less than the average meal size for these birds so several trials could be conducted in a short time.
8. The rate of improvement in shift learning was much greater when the shift learning followed stay learning than when the shift learning came first. This may represent a ceiling effect, since those birds who learned to shift first and showed lower rates of improvement began training at relatively high levels of shift behavior. Alternatively, this difference could represent some more basic difference in the learning process.
9. D. S. Olton and P. Schlosberg, *J. Comp. Physiol. Psychol.* **92**, 609 (1978).
10. D. S. Olton *et al.*, in *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*, A. C. Kamil and T. D. Sargent, Eds. (Garland, New York, 1981), pp. 333–354.
11. R. A. Hinde and J. Stevenson-Hinde, *Constraints on Learning* (Academic Press, New York, 1973); M. E. P. Seligman and J. L. Hager, *Biological Boundaries of Learning* (Prentice-Hall, Englewood Cliffs, N.J., 1972).
12. Supported by grants from the National Science Foundation and the Syracuse University Undergraduate Honors Program. We also acknowledge the Department of the Interior Fish and Wildlife Service and the Arizona Department of Fish and Game for permits. We thank C. L. Gass, T. Goldsmith, B. Heinrich, J. Krebs, S. E. G. Lea, W. Roberts, and S. Shettleworth for their comments on an earlier version of this report.

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Sex Pheromone of the Winter Moth, a Geometrid with Unusually Low Temperature Precopulatory Responses

Abstract. *The sex pheromone for the winter moth,* Operophtera brumata *(L.), has been identified as the novel compound (Z,Z,Z)-1,3,6,9-nonadecatetraene. The male moths respond to the pheromone at low temperatures (4° to 15°C) and exhibit an upper response limit that coincides with the lower response limit for other reported moth sex pheromone systems. The pheromone attracted two other geometrid species,* O. bruceata *(Bruce spanworm) and* O. occidentalis.

The winter moth *Operophtera brumata* (L.) is a common forest pest in Europe and was accidently introduced into Canada in the early 1930's. It has become a serious defoliator of oak, elm, flowering plum, apple, and filbert in expanding areas of eastern and western Canada and in the northwestern United States. A trap including synthetic sex pheromone of this species would have immediate utility in monitoring the spread of this pest, and an analysis of this moth's sex pheromone system would be important for other reasons as well. Although sex pheromones have been reported for species in most other lepidopteran families, there has been a conspicuous absence of characterized pheromones for any species in the Geometridae. Since pupal diapause of the winter moth is broken only in late fall when temperatures drop to about 7°C (*1*), the wingless female moths are dependent on a mating communication system that must function at temperatures well below the lowest temperature (around 16°C) at which males of most other species respond to their pheromones (*2*).

A previous study showed that a sex pheromone system was utilized by the winter moth (*3*). Using behavioral assays and electroantennagraphy (EAG) on abdominal tip extracts from female winter moths, we have now identified a novel sex pheromone, (*Z,Z,Z*)-1,3,6,9-nonadecatetraene **1**. This compound elicits the full range of precopulatory behavioral responses in flight tunnel bioassays and, in Nova Scotia, was as active as live females in attracting males to traps. The males responded to pheromone in the flight tunnel at temperatures as low as 4°C, but were unresponsive at temperatures above 15°C.

A sample of crude extract from the abdominal tips of 10,000 female winter moths (*4*) was subjected to chromatography on Florisil (~ 48 g) and eluted with 0, 1, 5, and 10 percent diethyl ether in Skelly B. EAG analysis (*5*) with male moths showed large antennal responses only to the fraction eluted with 1 percent diethyl ether in Skelly B. A portion of the active fraction was injected onto a gas-liquid chromatography (GLC) column (OV-101, 180°C) (*6*), and the effluent was collected at 2-minute intervals in glass capillary tubes. EAG analysis showed activity (5 mV) only in the 8- to 10-minute fraction (retention time of nonadecane was 9.15 minutes). The material obtained at 8 to 10 minutes was injected onto a polar XF-1150 column (160°C) (*6*), and the effluent was collected in 1-minute fractions. High EAG activity (8 mV) was elicited only with the 4- to 5-minute fraction (nonadecane, 2.9 minutes; heneicosane, 5.6 minutes). The active material collected from both GLC columns was used for the subsequent analyses.

Injection of the collected active material produced a peak corresponding to a

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