

References and Notes

1. This illusory perception of motion ("apparent motion") has an extensive history, some of it summarized in E. G. Boring, *Sensation and Perception in the History of Experimental Psychology* (Appleton-Century-Crofts, New York, 1942).
2. Restrictions on the visual transformations are described in P. A. Kolars, *Aspects of Motion Perception* (Pergamon, New York, 1972).
3. Colored flashes were alternated by several early workers, including M. Wertheimer, H. G. van der Waals and C. O. Roelofs, and P. C. Squires [cited in Kolars (2)]. They reported that the moving shapes changed color but did not describe how they changed. A recent study demonstrates motion effects even between spectral lights near threshold [D. H. Foster and I. I. M. Idris, *Vision Res.* 14, 35 (1974)].
4. Colored papers are polychromatic but have a dominant wavelength. The papers used were Color Aid 17 (yellow), 49 (red), 129 (blue), and 177 (green).
5. The gray alternative would not be shown by a monochromator setting. It was inquired after and never reported.
6. Color Aid 49 and 65 (red), and 161 and 177 (green).
7. For example, C. McCullough, *Science* 149, 1115 (1965); L. S. Fidell, *Percept. Psychophys.* 8, 235 (1970); several papers at the annual meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Florida, April 1974. Critical of the dual-purpose hypothesis are J. E. W. Mayhew and S. M. Anstis, *Percept. Psychophys.* 12, 77 (1972); J. Hirsch and G. M. Murch, *ibid.* 11, 406 (1972); R. Over, N. Long, W. Lovegrove, *ibid.* 13, 534 (1973).
8. P. A. Kolars, in *Recognizing Patterns: Studies in Living and Automatic Systems*, P. A. Kolars and M. Eden, Eds. (MIT Press, Cambridge, Mass., 1968), p. 35.
9. A full description of measurements on the smooth continuity of shape change is in preparation by P. A. Kolars and M. von Grunau.
10. We thank N. Goodman for stimulating this inquiry. The work was supported by grant A 7655 from the National Research Council of Canada. M.v.G. was supported in part by a predoctoral fellowship from the National Research Council of Canada.

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Innate Recognition of Coral Snake Pattern by a Possible Avian Predator

Abstract. *Inexperienced hand-reared motmots avoided a pattern of red and yellow rings but readily attacked a pattern of green and blue rings and also one of red and yellow stripes. The motmots' avoidance of the "coral snake" pattern indicates that mimic snake species can derive protection from some potential predators.*

A large complex of neotropical snakes from at least two families have ringed or banded patterns which usually involve red, yellow (or white), and black, but sometimes involve only two of these colors. They tend to be relatively small snakes, the majority being only 1 m or less in length (1, 2). Among these are the "true" coral snakes—the front-fanged elapid genera *Micrurus* and *Leptomicrurus*, whose venom can kill a small bird or mammal in minutes (1). Others, such as the rear-fanged colubrid genera *Erythrolamprus* and *Rhinobothrium*, are also venomous, but possess somewhat less virulent poison. Still others, like the colubrid *Lampropeltis*, are nonvenomous (2).

Considerable controversy exists in the literature as to whether this complex involves any mimicry at all, and if so, what kinds are included (1–4). Many believe that the true coral snakes are aposematically colored and serve as models for both Batesian and Müllerian mimics [for example, see (4)]. Wickler (1) proposed another interpretation, suggesting that if mimicry depends on predator learning, *Micrurus* and its allies are too deadly to serve as models; hence they are instead mimics of the more mildly poisonous rear-fanged

colubrids of the complex. This he termed Mertensian mimicry. He also stated that there was no evidence that any predator can recognize a coral snake innately. The experiments described here now demonstrate that hand-reared turquoise-browed motmots (*Eumomota superciliosa*) do have an innate aversion to a generalized coral snake

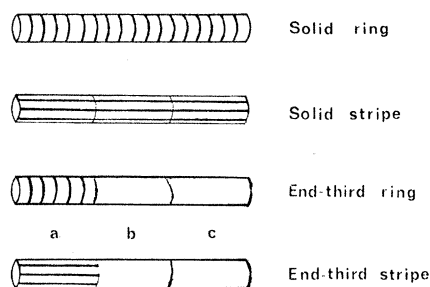


Fig. 1. Models used in the experiments, showing both solid and end-third forms. The ring pattern was given both as wide yellow and narrow red rings and as wide green and narrow blue rings. The striped pattern was given only as wide yellow and narrow red stripes. The models were divided into thirds by light pencil marks to aid in recording the location of the pecks; the birds did not peck at these marks. In the end-third models, (a) refers to the patterned third, (b) to the middle, and (c) to the other end.

pattern. This motmot species, a neotropical relative of the kingfishers that inhabits dry forest regions from México to Costa Rica, regularly eats lizards (5) and probably small snakes as well. *Micrurus* species and several of their mimic forms are common throughout the motmots' range.

Nine young motmots from four broods were removed from their nest burrows at ages ranging from 6 to 20 days and raised in the laboratory until they were old enough to catch their own prey. Each brood was kept in a separate cage made of hardware cloth on wooden frames and measuring 91 by 46 by 46 cm. The experiments consisted of placing a cylindrical wooden model (8.2 cm long and 1 cm in diameter) on the floor of a cage and recording the number and location of the birds' pecks for a 5-minute period. Models were painted with nontoxic tempera colors in the following patterns: yellow with red rings, yellow with red stripes, green with blue rings. Two models were made for each pattern: a "solid" model completely covered with the pattern and an "end-third" model in which only one end was painted, the other two-thirds being plain wood (Fig. 1).

Experiments with other models showed that the motmots had no hesitation in pecking at plain red, yellow, green, blue, or unpainted wooden models (6). However, the birds' initial reaction to the solid yellow and red ring model was one of avoidance: all flew up to the opposite corner of the cage and in many cases gave alarm notes. Only one bird approached this model voluntarily, twice landing about 10 cm away but immediately taking off again in apparent fright. No motmot made any attempt to peck at this model (Table 1). By contrast, the birds readily attacked the solid yellow and red stripe model, even though the colored bands had the same widths as those of the ring model, and hence the proportion of the two colors was also the same. The results for the solid green and blue ring model show that the birds were not inhibited by the ring pattern per se.

Similarly, in the responses to the end-third models (Table 1) the birds directed most of their pecks at the patterned third (Fig. 1a) of both the striped and the green and blue ring models, yet gave a highly significant response to the end farthest away from the pattern in the yellow and red ring model.

Table 1. Results of six experiments with wooden models (see Fig. 1). The end-third model with yellow and red rings received significantly more pecks at the unpatterned end (Fig. 1c) than at the patterned end ($P < .01$); in addition, the response to this model was significantly different at $P < .01$ from the responses to either of the other two end-third models.

Pattern	Pecks at end-third models				Pecks at solid models
	Total	Percentage at			
		a	b	c	
Yellow and red ring	79	15.19	5.06	79.75	0
Yellow and red stripe	90	46.81	14.89	38.30	60
Green and blue ring	33	66.67	0.00	33.33	89

Evidently this aversion to a yellow and red ring pattern is innate; since motmots are burrow nesters, the experimental birds had had no opportunity to see this pattern prior to their capture.

It seems unlikely that this is a response to a wasp pattern, as adult motmots regularly take a wide variety of hymenopterans, including the inch-long *Pepsis*, with no apparent difficulty (7). Indeed, motmots seem remarkably resistant to the chemical defenses of most insects (5, 7). However, coral snakes might well prove dangerous to motmots. They tend to be secretive and during the day are sometimes encountered partly concealed in forest litter. A motmot attacking a small exposed portion of a coral snake would be in danger of being bitten, especially if that portion did not include the head. Motmots have a heavy, powerful bill but very small feet which lack the heavy, protecting scutes of a hawk or an owl. Thus even a small-mouthed rear-fanged snake might successfully inject its venom if a motmot failed in its initial attack.

The motmots used in these experiments came from northwestern Costa Rica, where both the elapid *Micrurus nigrocinctus* and the very similar rear-fanged colubrid *Erythrolamprus bizona* occur (2). Venom from either of these could probably kill a turquoise-browed motmot. Moreover, there is apparently no mildly poisonous species with a coral snake pattern living in this area, and hence no opportunity for motmots of this population to learn by experience to avoid this pattern. Their innate ability to recognize and avoid such a pattern is thus adaptive.

There have been a few published reports of other avian predators capturing either *Micrurus* (8) or a non-venomous mimic (9). This negative evidence shows that in these instances there was no safety to be gained by being a member of the coral snake

complex. In order for mimicry to be effective, there must be predator avoidance of the character mimicked, and provided there is also generalization by the predator, it is irrelevant to the safety of the mimics whether this avoidance is innate or learned. The motmots' innate aversion to a generalized coral snake pattern is the first positive evidence that such protection exists for members of the coral snake complex against avian predators. An innate response to coral snakes has been suggested for at least one mammalian predator (10); further tests should be

done with other small potential predators to find out whether this recognition is a more general phenomenon. Perhaps the complicated mechanism of Mertensian mimicry is unnecessary to explain the existence of the coral snake complex in the neotropics.

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References and Notes

1. W. Wickler, *Mimicry in Plants and Animals* (World University Library, London, 1968), pp. 111-121.
2. J. H. Savage and J. L. Vial, *Rev. Biol. Trop.* **21**, 295 (1974).
3. B. Brattstrom, *Evolution* **9**, 217 (1955); E. R. Dunn, *ibid.* **8**, 97 (1954); M. K. Hecht and D. Marien, *J. Morphol.* **98**, 335 (1956).
4. R. Mertens, *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* **84**, 541 (1966).
5. A. F. Skutch, *Auk* **64**, 201 (1947).
6. S. M. Smith, in preparation.
7. F. G. Stiles, unpublished field notes.
8. T. R. Howell, *Condor* **59**, 74 (1957); N. G. Smith, *Copeia* **1969**, 402 (1969).
9. F. H. Pough, Jr., *Copeia* **1964**, 223 (1964).
10. F. R. Gehlbach, *Forma Functio* **5**, 311 (1972).
11. I thank F. G. Stiles for his help in finding and excavating the nests.

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Single Gene Cricket Mutations: Effects on Behavior, Sensilla, Sensory Neurons, and Identified Interneurons

Abstract. *Crickets are suitable for studying the effects of single gene mutations on single nerve cells. In one mutant, three classes of sensilla are lost sequentially. The absence of one class of mechanoreceptors throughout postembryonic development deprives certain sensory neurons of normal stimulation and results in abnormal physiological and structural development of an identified interneuron.*

Genetic manipulations can be used to investigate the role of genes in the construction of the nervous system and to produce lesions for analyzing the operation or the development of neural circuits. Current neurogenetics is based primarily on research with animals such as mice, *Drosophila*, *Paramecium*, *Daphnia*, and nematodes, in which it is difficult or impossible to study the physiology of particular neurons (1, 2). Mutations can be easily generated in crickets, however, and their neurons are amenable to physiological analysis. They are fecund, with females producing up to 2000 offspring, and have a reasonably short generation time (~6 weeks at 35°C). Eggs hatch into *Drosophila*-sized nymphs, which have a large behavioral repertoire and can be subjected to mass selection techniques. Interesting mutants can be studied as

adults, when their many large, identified neurons are easily accessible for physiological and structural investigation (3-6).

In this report, techniques are described for inducing mutations and screening for behavioral mutants. Mutants that fail to make the evasion response to stimulation of the cerci (posterior sensory appendages) have been isolated. The behavior involves an intensively studied circuit including sensilla, sensory neurons, identified interneurons, and identified motor neurons. One such mutant lacks filiform hairs, the mechanoreceptors that initiate the evasion response. After molting to adulthood, it selectively loses each additional class of sensilla save one. This allows selective study of the behavioral roles and connectivity within the nervous system of each class of sensilla.