wings with a black felt-tipped marker. Flies were first immobilized by chilling them at −10°C for about 30 seconds.

12. To determine that pen markings on the wing do not directly cause increased mortality, we maintained 20 flies, 10 of which we marked, within a Plexiglas cage. Mean age at death for each group did not differ (Mann-Whitney U test). Further, observations confirmed that flies did not behave differently after marking, nor was their ability to flee spiders hampered.
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A Tephritid Fly Mimics the Territorial Displays of Its Jumping Spider Predators

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The tephritid fly *Zonosemata vittigera* (Coquillett) has a leg-like pattern on its wings and a wing-waving display that together mimic the agonistic territorial displays of jumping spiders (Salticidae). *Zonosemata* flies initiate this display when stalked by jumping spiders, causing the spiders to display back and retreat. Wing transplant experiments showed that both the wing pattern and wing-waving displays are necessary for effective mimicry: *Zonosemata* flies with transplanted house fly wings and house flies with transplanted *Zonosemata* wings were attacked by jumping spiders. Similar experiments showed that this mimicry does not protect *Zonosemata* against nonsalticid predators. This is a novel form of sign stimulus mimicry that may occur more generally.

MOST FORMS OF MIMICRY, SUCH as cryptic coloration or Batesian and Müllerian systems, confer protection against a wide array of predators (*1*). We describe a novel form of mimicry in which an organism mimics its major predator and thereby reduces the risk of being eaten by it. A tephritid fly, by mimicking the stereotyped aggressive behavior of one family of spiders, can escape from spiders of this family but not from other predators.

The fly *Zonosemata vittigera* (Diptera: Tephritidae) is purported to mimic jumping spiders (Araneae: Salticidae) (*2, 3*). Both sexes have dark wing bands, which resemble spider legs, and false eyespots on the end of the abdomen. When disturbed, these flies hold their wings perpendicular to the body and wave them up and down (Fig. 1A); this resembles the agonistic leg-waving behavior typical of the jumping spiders. However, there have been no experimental demonstrations that *Zonosemata* is a spider mimic. Many flies have dark wing markings and wing-flicking displays, so *Zonosemata* might fortuitously resemble jumping spiders, but not gain protection from predators by these features. If *Zonosemata* is in fact a jumping spider mimic, it is not clear what types of predators are deterred. Since salticids are quick and have a poisonous bite, it has been suggested that a salticid mimic may be shunned by many vertebrate and arthropod predators (*3*).

Another possibility, which had not been suggested, is that *Zonosemata* displays may specifically mimic salticid territorial displays, and be effective only against salticid predators (*4*). Many salticids defend "privacy spheres" around themselves. When two meet they usually initially perform agonistic displays (which may turn into courtship displays depending upon sex and species) (*5*). These displays can be performed by juveniles and adults of both sexes and occur within and between species. Although the precise details of these stereotyped behavioral displays vary intraspecifically, salticid agonistic displays generally commence with leg-waving (*6*).

To test the effect of the wing pattern and the wing-waving display on the behavior of jumping spiders and other potential predators, we transplanted wings between house flies (*Musca domestica*) and *Zonosemata* flies (*7*). House fly wings are the same general size and shape as *Zonosemata* wings, but they lack pattern. After this operation, the flies retained complete movement of their wings, and could display and fly normally (Fig. 1B).

Behavioral trials between jumping spiders and flies were conducted for 5 minutes in a glass-topped arena (*8*). Jumping spiders were collected on or around *Zonosemata* host plant (silver leaf nightshade, *Solanum elaeagnifolium*). Twenty jumping spiders representing 11 species (*9*) were each presented with five treatments: normal *Zonosemata*, *Zonosemata* with other *Zonosemata* wings (sham operation), *Zonosemata* with house fly wings, house flies with *Zonosemata* wings, and normal house flies. Each spider was presented with these treatments in a random order. All jumping spiders were hungry when tested: they were given water but no food for 2 days before the trial. Individual spiders were never tested more than twice in one day.

The wing pattern had a profound effect upon jumping spider behavior (Fig. 2). Normal *Zonosemata* and the sham-operated control flies were attacked or killed less frequently than flies in the three remaining treatments (*10*). There was no statistically significant difference in the jumping spiders' responses to the normal *Zonosemata* flies and the sham-operated control flies (homogeneity test, $G = 3.28$, $P > 0.1$), indicating that the operation itself did not affect spider responses. Jumping spiders began stalking these flies within seconds after the trial began. When the spider approached to within about 5 cm, *Zonosemata* flies usually began a vigorous wing-waving display. In response, the jumping spiders abruptly stopped stalking and waved their legs at the flies. The flies backed away in a zigzag fashion while waving their wings and flew off. Most jumping spiders made no further stalking attempts during the remaining 5 minutes. Jumping spiders were repelled from both the front and back of the flies. In

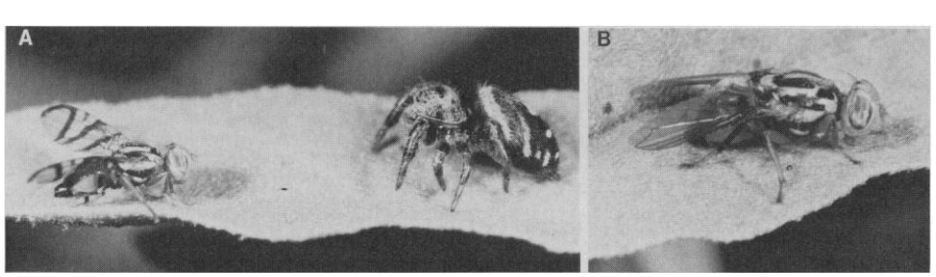

Fig. 1. (**A**) A female *Zonosemata vittigera* beginning its wing-waving display toward a stalking jumping spider (*Phidippus apacheanus*). The jumping spider stopped stalking, waved its legs at the fly, and then retreated. (**B**) A *Zonosemata vittigera* fly with transplanted house fly wings. Such flies can display normally and fly.

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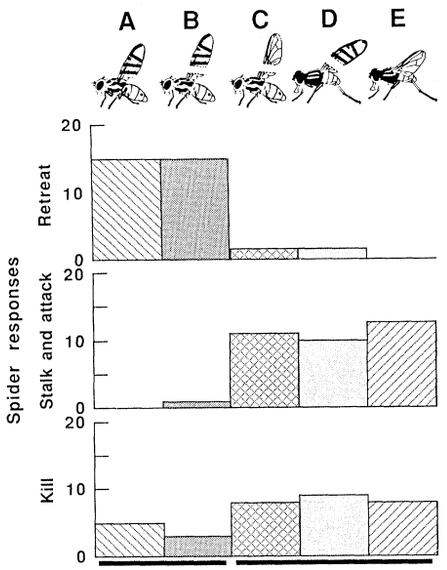

Fig. 2. Behavioral responses of jumping spiders to fly presentations. The response is the highest level of aggression attained during 5 minutes of behavioral interaction in a test arena. The fly treatments are: A, normal *Zonosemata*; B, *Zonosemata* with *Zonosemata* wings glued on (control for the operation); C, *Zonosemata* with house fly wings; D, house fly with *Zonosemata* wings; and E, normal house fly. Sample sizes are 20 for each fly treatment. The bars connect homogeneous groups (G tests, P's > 0.1). All other combinations are heterogeneous (all P's < 0.01).

six trials the jumping spiders stalked from behind, apparently unobserved by the fly. The flies gave spontaneous wing-flicks (about one series in 10 seconds). The jumping spiders stopped stalking, waved their legs, and backed away.

However, not all *Zonosemata* flies with the wing pattern were immune to jumping spider attacks: of the 40 *Zonosemata* in treatments A and B, 2 were attacked, and 8 others were killed. This is partly a reflection of the conservative bias used in classifying the behavioral responses: spiders were scored on their highest level of aggression during the 5-minute experiment. Of these ten flies that were attacked, six probably would have escaped if unconfined since they repeatedly displayed and repelled attacks (a mean of 2.1 effective displays). Also, even though they were eventually attacked, the flies displaying with patterned wings were afforded some protection: the latency to the first attack was longer for these six flies than for *Zonosemata* flies with house fly wings (median latency was 44 seconds versus 11 seconds; Mann-Whitney $U = 61$, $P < 0.005$). The remaining four flies were attacked so quickly they had no chance to display.

In contrast, the spiders responded much more aggressively toward the three other types of flies (*Zonosemata* with house fly wings, house flies with *Zonosemata* wings, and normal house flies). Of particular interest, *Zonosemata* with house fly wings displayed identically to normal *Zonosemata* flies, but this never elicited the leg-waving displays from spiders, and all but one were attacked or killed. House flies with *Zonosemata* wings held the wings flat over their bodies: the pattern was not visible to spiders, which never displayed toward these flies.

To determine if these displays also protected *Zonosemata* flies against other potential predators, we performed similar experiments using nonsalticid spiders (*Oxyopes salticus*), mantids (*Mantis religiosa*), assassin bugs (*Pselliopus zebra*), and whiptail lizards (*Cnemidophorous uniparens*; Arizona Research Permit 089). All predators were caught on or around the host plant of *Zonosemata*. These predators were presented with three fly treatments (A, C, and E of Fig. 2). The same testing protocol was used except that the test chamber sizes were varied to accommodate the different sizes of these predators (*11*).

The *Zonosemata* display is not effective against these four types of predators (Table 1). None were deterred by displaying flies, as occurred with jumping spiders. For each predator, there was no statistically significant difference in capture times for the three treatment groups (pairwise Mann-Whitney U tests, all P's > 0.05).

In summary, *Zonosemata* is a specialized mimic. Rather than conferring protection against many types of visual predators, this jumping spider mimicry is effective only against jumping spiders. The neurological mechanism of this mimicry is clear: jumping spiders possess feature detectors in the retina of their central anterior-median eyes which are excited by waving leg-like patterns (*12*). Model presentations to salticids have shown that leg-like patterns are potent releasers that cause jumping spiders to abruptly stop what they are doing (usually stalking) and display back (*13*). Thus, the *Zonosemata* display mimics a sign stimulus recognized by salticids but not by other predators. This accounts for the extreme specificity of the protection: other examples of sign stimulus mimicry are effective against a similarly narrow range of signal receivers (*14*).

How could this mimicry syndrome have evolved? Wing markings and wing-flicking displays are common among acalyptrate flies, and are especially prominent in the courtship displays of tephritid flies (*15*). Salticids can occur at very high densities, and they can exert strong predation pressures on many insects, such as tephritid flies, that spend time on exposed vegetation (*16*). It is possible that the defensive display of *Zonosemata* derived from courtship behavior, since refinements of displays that deterred jumping spider attacks could confer large survivorship advantages. A cursory glance at a museum drawer of flies reveals many with leg-like wing patterns. Thus, jumping spider mimicry may be a widespread phenomenon among many species of flies. Analogous defenses might be expected in other insects that are also highly apparent to a specific class of predators.

Table 1. Capture times for three fly treatments by potential predators of *Zonosemata*. The fly treatment symbols are the same as for Fig. 2. For each predator there is no statistically significant difference between treatment medians (pairwise Mann-Whitney U tests, all P's > 0.05).

Fly treatment	Sample (n)	Median capture time (seconds)	Range (seconds)
Nonsalticid spider Oxyopes salticus			
A	10	80	16–207
C	10	77	32–149
E	10	56	32–292
Assassin bug Pselliopus zebra			
A	8	234	39–632
C	8	309	52–889
E	8	162	34–736
Mantis Mantis religiosa			
A	12	88	29–435
C	12	64	11–215
E	12	94	41–341
Whiptail lizard Cnemidophorous uniparens			
A	10	101	47–355
C	10	81	24–370
E	10	92	9–119

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7. *Zonosemata* flies were obtained by gently sweep-netting the host plant, silver leaf nightshade (*Solanum elaeagnifolium*). Flies were collected between 15 June and 5 August 1986, along State Line Road near Rodeo, NM, and briefly maintained in a 2 by 1 by 1 m terrarium that contained potted nightshade and water, dry powdered milk, and a honey and water solution. Flies were cooled in a refrigerator until inactive, then held immobile on an operating board with paper strips and insect pins. Their wings were cut off distal to a line connecting the medial cell and the intersection of veins R_{2+3} and R_{4+5} (Comstock terminology). Wings from donor flies were

glued on to the remaining wing stubs with Elmer's White Glue.

8. A glass-topped plaster of paris test arena measured 12 cm by 8 cm and 2 cm deep. A partition divided the arena in half. A spider was introduced into one half and the fly into the other half through small entrance tunnels. During a 10-minute acclimation period they could not see each other. The trial began after the partition was slowly removed.
9. The following salticids were tested (species name followed by the numbers of individuals: J, juvenile; M, adult male; F, adult female): *Metaphidippus arizonensis*, 1 F; *Metaphidippus manni*, 1 F, 1 M; *Metaphidippus* sp. A, 2 F; *Thiodina* new species, 2 J, 1 M; *Eris aurantia* (probably), 2 J; *Sassacus papenhoei*, 1 F; *Habronattus* sp. A, 1 J, 1 F; *Phidippus apacheanus*, 3 J; *Phidippus* sp. A, 1 J; *Phidippus* sp. B, 2 J; *Phidippus* sp. C, 1 J.
10. Treatments (A + B) and (C + D + E) constituted maximally nonsignificant homogeneous subsets of the data [a posteriori G tests with $P = 0.05$; R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969)].
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17. This research was stimulated by the photographs of *Zonosemata* published by T. Eisner. We worked at the Southwestern Research Station of the American Museum of Natural History, and we thank W. Sherbrooke, P. Limberger, and the Remingtons for logistical support. Partial funding was provided by the Theodore Roosevelt Memorial Fund of the American Museum of Natural History and Princeton University. We are grateful to W. Gersch, D. Richman and V. Roth for help with spider identification, and to T. Eisner, J. Gould, P. Harvey, T. Ives, R. Jackson, L. Hamilton, B. Lyon, K. Monahan, N. Pierce, R. Prokopy, J. Seger, B. Tomberlin, E. Wachmann and two reviewers for helpful discussions and thoughtful readings of the manuscript. Special thanks to E. Wachmann for assistance with photography and to S. Cover for help making the testing arenas.

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Newly Identified 'Glutamate Interneurons' and Their Role in Locomotion in the Lamprey Spinal Cord

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A new class of excitatory premotor interneurons that are important in the generation of locomotion in the lamprey has now been described. In the isolated spinal cord, these neurons act simultaneously with their postsynaptic motoneurons during fictive swimming. They are small and numerous, and they monosynaptically excite both motoneurons and inhibitory premotor interneurons. The excitatory postsynaptic potentials are depressed by an antagonist of excitatory amino acids. These interneurons receive reticulospinal input from the brain stem and polysynaptic input from skin afferents. A model of the network underlying locomotion based on the synaptic interactions of these neurons can now be proposed for the lamprey.

TO HELP US UNDERSTAND HOW THE vertebrate nervous system controls complex motor acts such as locomotion, an experimental model using a lower vertebrate, the lamprey, has been developed (*1, 2*). The motor pattern underlying locomotion can be elicited in the isolated spinal cord in vitro (*3*). During each fictive swim cycle, motoneurons (MNs) exhibit an excitatory phase followed by an inhibitory phase (*4, 5*). Interneurons contributing to the inhibitory phase have been characterized (*6*), and indirect evidence suggests that rhythmically active excitatory interneurons (EINs) contribute to the excitatory phase by an activation of excitatory amino acid receptors (*7*). Using paired intracellular recordings, we have now identified such EINs.

The experimental preparation consisted of pieces of spinal cord attached to the notochord, five segments long, from adult silver lampreys (*Ichthyomyzon unicuspis*). The recording chamber was perfused with cooled (9°C) physiological saline solution (*8*). MNs were impaled with micropipettes and identified by their characteristic action potentials in a ventral root recorded with a suction electrode. A second micropipette was used to impale neurons randomly within the same or an adjacent rostral segment and to test for synaptic interactions with the MN (*6*).

Intracellular stimulation of an EIN (Fig. 1B) elicited excitatory postsynaptic potentials (EPSPs) (Fig. 1A) in an MN (Fig. 1B). The EPSPs produced in MNs by stimulation of EINs were considered monosynaptic because they followed 10-Hz stimulation with constant size, shape, and latency (*9*). The amplitudes of the EPSPs evoked by premotor EINs ($n = 31$) ranged from 0.2 to 1.9 mV [0.7 ± 0.4 mV (mean ± SD)]. The EPSPs varied in time course: time to peak ranged from 3.4 to 16.4 msec (7.5 ± 3.6 msec), and duration at one-half peak amplitude ranged from 8.4 to 70 msec (30.0 ± 19.1 msec) (*10*). In addition, we also found interneurons that excited inhibitory interneurons: lateral interneurons (Fig. 1D) and inhibitory interneurons that have a contralaterally and caudally projecting axon (CCINs) (Fig. 1E). Lateral interneurons are large cells with a descending axon (*11*) that inhibits CCINs (*6*). CCINs inhibit MNs and interneurons on the opposite side of the spinal cord (*6*). The EPSPs in these inhibitory interneurons produced by stimulation of EINs were considered monosynaptic according to the same criteria by which MNs were judged. Single EINs might thus contact all three classes of postsynaptic cells, but this possibility has not been directly demonstrated.

To test if the EPSPs from EINs to MNs were mediated by excitatory amino acid receptors, a small volume (10 nl) of 50 m*M* *cis*-2,3-piperidine dicarboxylate, an antagonist acting on all three subtypes of excitatory amino acid receptors [*N*-methyl-D-aspartate (NMDA), kainate, and quisqualate (*12*)], was applied to the surface of the spinal cord from a pressure pipette (*13*). As found in all six tested pairs and as in Fig. 1C, the EPSPs were reduced by the piperidine dicarboxylate, thus suggesting that the EINs activate receptors for excitatory amino acids.

The EINs were located within the main area of neuron cell bodies, probably corresponding to the ventral horn and adjacent intermediate area of higher vertebrates. The cells had transversely oriented dendrites. Like the other dye-injected EINs ($n = 15$), the soma of the EIN in Fig. 1B was about 10 μm in diameter, making these cells among the smallest identified neurons in the lamprey spinal cord. The axons of EINs were thin, usually less than 2 μm in diameter, and in several cases the axonal action potentials could be recorded with a suction electrode on the spinal cord three to five segments caudal to the cell body. Although

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