Tricking moths into revealing the computational underpinnings of sensory integration

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The hawkmoth *Manduca sexta*. Credit: Rob Felt/Georgia Institute of Technology

Our nervous systems are remarkable translators, channeling information from many sources and initiating appropriate behavioral responses.

But though we know how a lot about how neurons work, scientists do not fully understand how the nervous system integrates stimuli from different senses. You may smell smoke and feel heat, but how does the brain combining and interpret these different stimuli, signaling you to phone the fire department?

It turns out that insects are attractive models to investigate questions about integrating information from different sensory pathways. The hawkmoth, Manduca sexta, uses a long, trunk-like proboscis to drink up sweet nectar meals from obliging flowers. A research team led by University of Washington biology professor Tom Daniel has teased out how hawkmoths integrate signals from two sensory systems: vision and touch.

Their findings, published Oct. 24 in the *Proceedings of the National Academy of Sciences*, illustrate the computational basis of this integration, which may serve as a general model for insects, other animals and humans.

"Sensory integration remains one of the more interesting tasks that even simple nervous systems accomplish," said Daniel. "From tasks like reaching in humans to nectar-feeding in insects, our challenge has been developing experimental ways to reveal the mechanisms and circuitry that underlie combined visual and mechanical sensing."

The hawkmoth's proboscis is longer than its body, so it can probe deep within a flower to find nectar while the hawkmoth hovers above. Even as the flower sways and blows with the wind, hawkmoths have been observed adjusting their position to track with the flower's position.

Scientists can study tracking behavior in the laboratory using specially designed, artificial flowers constructed with their own small nectar pods. Hawkmoths respond to these pre-packaged dinners similarly to real flowers, and—if researchers manipulate the artificial flower to move when a hawkmoth is feeding—the hawkmoth adjusts its position to keep up.

In addition to its drinking duties, the proboscis is also a sensory organ, relaying information about the moving flower it is touching. To see how input from different sensory systems contributed to tracking behavior, Daniel's team modified the artificial flowers to simultaneously deliver contradictory visual and tactile cues: the flower's petals, which the hawkmoth follows using its eyes, move independently from the nectar pod, which the hawkmoth proboscis touches. By studying how moths respond to discordant visual and touch signals, they hoped to decipher how the hawkmoth brain processes and combines inputs from both sensory systems.

"Typically, to study how a particular sense contributes to a behavior, scientists try to design experiments in which the animal only receives that one kind of sensory cue," said UW postdoctoral researcher Eatai Roth, who is lead author on the paper. "But this doesn't reflect what's happening when an ensemble of senses contribute concurrently. Our approach—sensory conflict—bombards the animal with rich multisensory cues simultaneously. This allows us to model how information is processed and combined concurrently across different senses."

Daniel and his team tested how well hawkmoths tracked while feeding on the discordant flower. When the nectar chamber moved but the rest of the flower was still, the moths were generally able to sway in response to their moving meal. But when they kept the nectar chamber still and moved the flower petals, moths only swayed slightly.

This indicated that, for feeding, tactile information transmitted by the proboscis may be a more important sensory input than vision.

"In nature, the visual and touch cues largely agree and either sense alone is enough for the job. Having both provides redundancy, a backup just in case," said Roth. "But when we present the moth with conflicting stimuli, it must decide how to balance the mismatched information—which cue to follow. And it turns out, quite surprisingly, that touch beats out vision in this sensory tug-of-war."

They measured hawkmoth positions during the tests and used these data to describe hawkmoth behavior in terms of a mathematical model. Though the sense of touch appeared to play a greater role in tracking behavior, moths do not rely on this sense alone. Their mathematical model indicated that the moth brain uses a simple additive or "linear summation" model to integrate signals from the proboscis and the eyes. And though moths rely heavily on the touch cues from the proboscis, the model suggests that both the visual and touch senses are acute enough for the moth to follow the flower.

The team used this model to predict how moths would behave in a new discordant setting in which the nectar chamber and flower were both moving, but quite differently. The researchers tested these predictions on a different set of hawkmoths, and they responded to this floral discord just as the model predicted. Daniel and his team believe that the mathematical underpinnings they describe here may represent a common mode of signal integration in animals.

More information: Eatai Roth et al, Integration of parallel mechanosensory and visual pathways resolved through sensory conflict, *Proceedings of the National Academy of Sciences* (2016). DOI: 10.1073/pnas.1522419113

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