

# What singing fruit flies can tell us about quick decisions

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When fruit flies court, the male chases the female as he vibrates his wings to produce roughly five-second serenades, or "bouts." The above video shows the male pursuing the female and moving his wing to produce a song. The song is composed of a buzzing sound known as a "sine" and a purring sound called a "pulse." The male switches off between the pulse and sine every several milliseconds, so that the two sounds seem almost simultaneous. The researchers found that, in general, males sang loudly — or produced more pulses — when females were farther away and moving quickly. Upon catching up to a female, males shifted to a song with more of the quieter sines. Most importantly, the researchers found that the neural circuits that guide the male's movement also

determine the pattern — the composition of pulses versus sines — of his song.  
Credit: Philip Coen, Princeton Neuroscience Institute

You wouldn't hear the mating song of the male fruit fly as you reached for the infested bananas in your kitchen. Yet, the neural activity behind the insect's amorous call could help scientists understand how you made the quick decision to pull your hand back from the tiny swarm.

Male [fruit flies](#) base the pitch and tempo of their mating song on the movement and behavior of their desired female, Princeton University researchers have discovered. In the animal kingdom, lusty warblers such as birds typically have a mating song with a stereotyped pattern. A fruit fly's song, however, is an unordered series of loud purrs and soft drones made by wing vibrations, the researchers reported in the journal *Nature*. A male adjusts his song in reaction to his specific environment, which in this case is the distance and speed of a female—the faster and farther away she's moving, the louder he "sings."

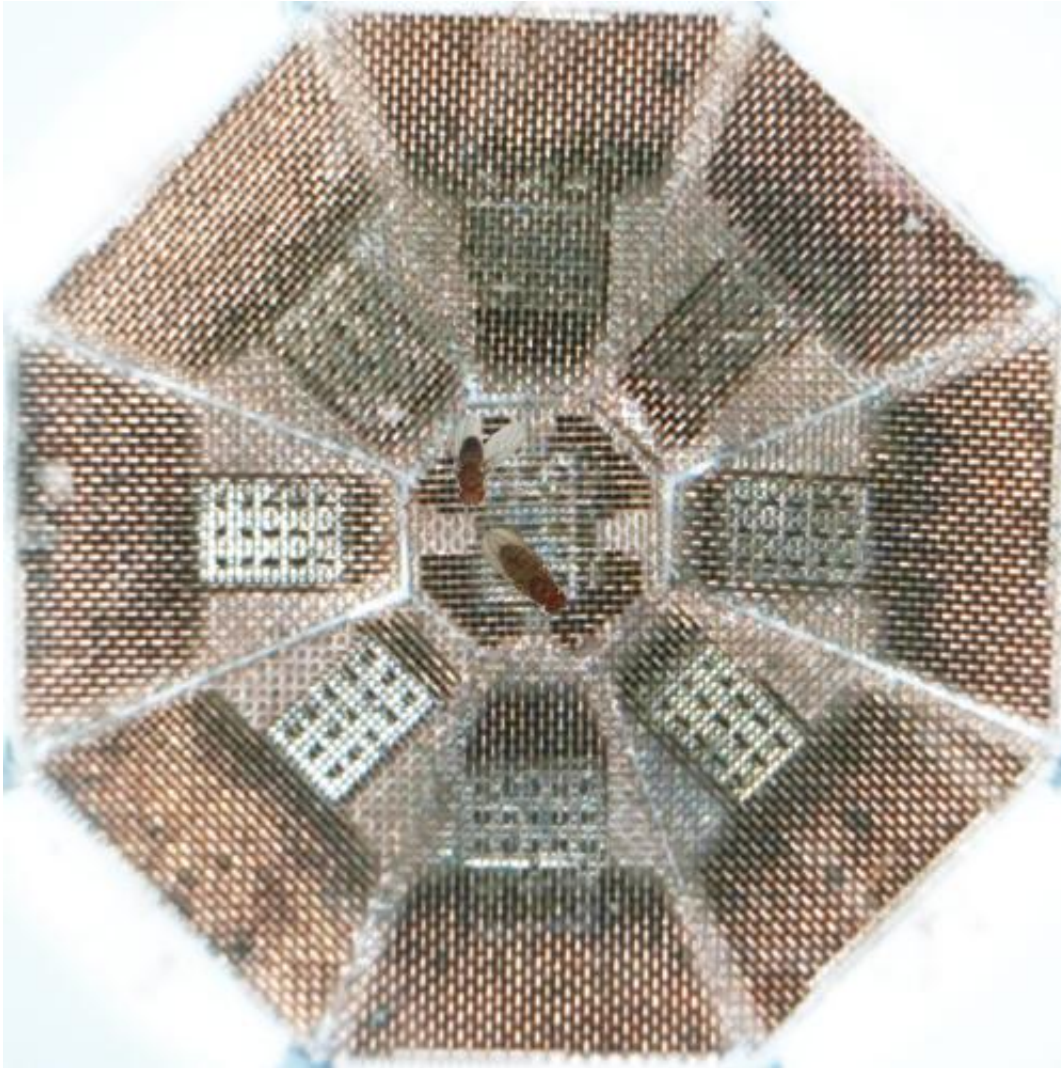
While the actors are small, the implications of these findings could be substantial for understanding rapid decision-making, explained corresponding author Mala Murthy, a Princeton assistant professor of molecular biology and the Princeton Neuroscience Institute. Fruit flies are a common model for studying the systems of more advanced beings such as humans, and have the basic components of more complex nervous systems, she said.

The researchers have provided a possible tool for studying the neural pathways behind how an organism engaged in a task adjusts its behavior to sudden changes, be it a leopard chasing a zigzagging gazelle, or a commuter navigating stop-and-go traffic, Murthy said. She and her co-authors created a model that could predict a fly's choice of song in

response to its changing environment, and identified the neural pathways involved in these decisions.

"Here we have natural courtship behavior and we have this discovery that males are using information about their sensory environment in real time to shape their song. That makes the fly system a unique model to study decision-making in a natural context," Murthy said.

"You can imagine that if a fly can integrate visual information quickly to modulate his song, the way in which it does that is probably a very basic equivalent of how a more complicated animal solves a similar problem," she said. "To figure out at the level of individual neurons how flies perform sensory-motor integration will give us insight into how a mammalian brain does it and, ultimately, maybe how a human brain does it."



Princeton University researchers have discovered that the pitch and tempo of the male fruit fly's mating song is based on environmental cues rather than a stereotyped pattern. These findings could be substantial for understanding rapid decision-making in more advanced beings such as humans. The researchers have provided a possible tool for studying the neural pathways behind how an organism engaged in a task adjusts its behavior to sudden changes, be it a leopard chasing a zigzagging gazelle, or a commuter navigating stop-and-go traffic. To capture the male fruit fly's mating song, the researchers constructed an octagonal chamber covered in copper mesh and fitted with nine high-fidelity microphones (above). The researchers then placed a sexually mature male and female in the chamber and recorded more than 100,000 song bouts. Credit: Philip Coen, Princeton Neuroscience Institute

Aravi Samuel, a Harvard University professor of neuroscience who studies the brain and behavior using roundworms and fruit fly larvae, said that the researchers conducted the kind of "rigorous" behavioral analysis that is essential to understanding the brain's circuitry.

"Neuroscience isn't just making electrical recordings of circuits or finding molecules that affect circuit properties," said Samuel, who is familiar with the research but had no role in it. "It also is about understanding the behavior itself, from sensory input to motor output. Understanding the computation the animal is making by studying the animal is the proper framework for future mechanistic studies."

The findings align with existing research that suggests that there is in fact a hidden pattern and predictability to seemingly random behavior, Murthy said. The researchers cited a 2010 paper in the journal *Science* that found that a person's movements are highly predictable. Researchers based at Northeastern University studied three months of cellphone data for 50,000 randomly selected people. They used phone company records of the cell towers each person passed by to determine where and how far an individual traveled. They found that a person's route and destination could be predicted 93 percent of the time on average, and no individual could be pegged less than 80 percent of the time.

In that same vein, variability in the songs of fruit flies and other animals had long been considered to be disruptions, or "noise," in the brain processes that produced those sounds, Murthy said. Like the movement of those cellphone customers, the songs were assumed to be random. Instead, the Princeton group's results show that the songs of fruit flies at least are deliberate and predictable reactions to the environment.

"No one expected that male fruit flies might be fine-tuning their courtship signals based on what the female is doing in real time," Murthy said. "We were able to test that for the first time and discover that

actually there's a very small number of sensory cues the male is using to shape his song structure. That overturns the canonical view that animal songs are variable simply because the nervous system is noisy."

Scientists who study behavior in larger animals and even humans should emulate the Princeton researchers in challenging the conventional wisdom regarding how those organisms behave, Samuel said. "People previously looked at randomness in fruit fly behavior and automatically assumed intrinsic stochasticity [randomness] in circuit performance," he said.

"Murthy and her colleagues challenged that assumption and found it to be false. Now, they have carefully delineated a computation with multiple inputs that they can follow into the brain in a much more rigorous way," Samuel continued. "They know that the animal sees its neighbors, quantifies its movements, and uses that to calculate the song produced. They established that the fly's whimsical behavior is actually quite predictable when you go through the trouble of identifying all the relevant inputs."

When fruit flies court, the male chases the female as he vibrates his wings to produce roughly five-second serenades. About 20 percent of the time he spends pursuing a young female goes toward producing these vibrations, which are composed of a purr, or "pulse," and a buzzing sound known as "sine." The male switches off between the pulse and sine every several milliseconds, so that the two sounds seem almost simultaneous to the human ear.

To capture these sounds, the researchers constructed an octagonal chamber covered in copper mesh and fitted with nine high-fidelity microphones. They recorded more than 100,000 song "bouts," or the seconds-long strings of vibrations males produce whilst wooing. Murthy worked with first author and graduate student Philip Coen, postdoctoral

researcher Jan Clemens and graduate student Diego Pacheco, all in the Princeton Neuroscience Institute; Andrew Weinstein, who received his bachelor's degree in molecular biology from Princeton in 2013; and Yi Deng, a former graduate student in Princeton's physics department and now at the University of Washington School of Medicine.

The researchers then placed a sexually mature male and female in the chamber to record the sounds of their courtship. The researchers genetically altered certain groups of flies so that they lacked specific senses. For instance, one group of males could not see, while another group was mute. Certain females were deaf, and nearly all the females were blind and invulnerable to pheromones to ensure that they responded selectively to a male's song.

The researchers found that, in general, males sang loudly—or produced more pulses—when females were farther away and moving quickly. Upon catching up to a female, males shifted to a song with more of the quieter sines. But various factors could change an encounter's outcome. For instance, males needed to be able to see the female to be attuned to her cues. Blind males and normal males plunged into darkness did not change their songs in response to female activity. Receptive females slowed down in response to song, while unreceptive females sped up. Independent of the female's behavior, however, both successful and unsuccessful males had a similar ability to adapt their song to a female's actions, Murthy said.

Importantly, the researchers found that the neural circuits that guide the male's movement also determine the pattern—the composition of pulses versus sines—of his song. One might assume that the male's visual neural circuits are at play because his song is a response to her movement, Murthy said. But when she and her colleagues prompted a male to sing in the absence of a female, his song pattern matched his motion. This arrangement could be for the sake of simplicity, she said.

Instead of the fly's many sensory circuits such as vision linking to the circuits for movement and singing, singing is determined solely by locomotion. In other words, Murthy said, the fly's dance determines his song.

"These fly songs have a lot of variability. Each time the male produces a bout of song to a female, it's slightly different from the one he produced before," Murthy said. "He measures his distance to the female fly and he uses information about her speed, which translates into his speed because he's following her and chasing her. He's constantly integrating those two pieces of information to determine exactly how to pattern his [song](#)."

"That kind of variability makes flies an attractive model to try to understand how the sensory environment influences behavior," Murthy said.

In humans, Samuel said, the influence of our surroundings on our behavior is so vast that we couldn't be completely conscious of it. Perhaps, like the fly, human behavior might be much more predictable than it seems if scientists could inventory all of the determinants of our actions with the same thoroughness that Murthy and her co-authors achieved for fruit flies.

"These researchers were able to show that in fact what is unpredictable at first glance can really be thought of as almost a deterministic calculation, just one with several inputs," Samuel said.

"We like to think of ourselves as something other than machines, and that our thoughts and actions aren't entirely prescribed by quantifiable inputs," he said. "But it's not impossible that we are unconscious of most of the inputs that we are processing. And if we are, we might be much more predictable and less capable of whimsy than we give ourselves



credit for. If we could stand outside ourselves, and plot all the input variables that go into our behaviors, we might find ourselves more like the predictable fruit fly, this would be paradigm shifting."

**More information:** The paper, "Dynamic sensory cues shape song structure in *Drosophila*," was published online in advance of print by *Nature* on March 5.

Provided by Princeton University

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