

(Figure 1C) was almost closed with the gate laterally open by less than 4 Å and the plug not detectably shifted [4]. However, the changes appeared to be sufficient to produce a small gap in front of the plug. The nascent chain was not visible, suggesting a flexible and extended conformation, and neither were the amino-terminal TM domains, indicating that they had been released into the hydrophobic phase. In contrast, the TM domain that had just entered the translocon (Figure 1D) was again detected as an extra density suggestive of a helix, which was intercalated into the lateral gate that was splayed open by ~12 Å. The plug had slightly moved, but remained inside the translocon, with gate opening providing most of the space for the passage of the chain.

These new cryo-EM snapshots reveal a spectrum of conformational states of SecYEG/Sec61 translocons at work. At the same time, they support a number of conclusions derived from more indirect biochemical experiments. What is still missing of course is the dynamics. It has been proposed that TM domain integration is the result of dynamic equilibration between the pore and the lipid environments [20], which is not detectable in static representations. I am thus looking forward to seeing a movie of the translocon in action.

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Animal Communication: Keep Your Wings Off My Food!

When foraging, male big brown bats produce ultrasonic social calls. The calls repel rival bats from the caller and its prey, and increase the caller's foraging success during their high-speed aerial excursions.

David R. Wilson

People have marveled for centuries at the ability of bats to hunt in complete darkness [1]. While navigating cluttered environments, they pursue prey with astounding agility and strike them with lethal precision. These remarkable feats are possible because of a complex biosonar system known as

'echolocation' [2,3]. During flight, bats utter loud calls in rapid succession (often up to 200 calls per second), and then use the returning echoes to decipher the location and salient features of objects in their environment [3]. Although powerful, echolocation is subject to a number of fundamental constraints. For example, bats must produce calls quickly enough to

resolve rapid movements by prey, but not so quickly that their returning echoes become masked by the next outgoing call [4]. They must also contend with the potentially masking effects of calls produced by other foraging bats [5]. Given these constraints, it may seem unlikely that flying bats would stress their vocal system further by producing and perceiving acoustic signals that are not used directly in echolocation. Yet, exciting new research in this issue of *Current Biology* by Genevieve Wright and colleagues [6] shows that foraging male big brown bats do supplement their echolocation calls during flight by producing social calls that repel rivals



Figure 1. Bat calls repel rivals while foraging.

Foraging male big brown bats, such as those shown here, produce ultrasonic social calls that repel rivals and increase the caller's hunting success. (Photo: Jessica Nelson.)

and increase the caller's hunting success (Figure 1).

For over 75 years, bioacoustic research on bats has concentrated on how individuals use echolocation to navigate their physical environment. Considerably less attention has been given to how bats use vocalizations to communicate with other bats, although this trend has begun to change in recent years. For example, we now know that echolocation calls may themselves communicate information about a caller's identity, age, family affiliation and sex [7,8]. Other research has shown that bats possess rich repertoires of social calls, which are distinct from those calls used in echolocation [9]. Common functions of social calls in bats include mediating aggressive interactions, attracting mates, signalling distress, and uniting females with their separated infants [10]. Given their diverse functions, it is not surprising that social calls are produced in a variety of contexts, yet rarely have they been shown to be produced during flight, when echolocation taxes the vocal communication system. Furthermore, the functions of the few social calls that are known to be produced during flight have only rarely been described [11,12], likely

owing to the immense challenge of ascribing ultrasonic calls that we cannot hear to rapidly flying bats that we cannot see.

Big brown bats (*Eptesicus fuscus*) are one of the most extensively studied species of bat in the world, particularly with respect to their echolocation system. Yet, we still know relatively little about how they use vocalizations for social communication. Previous investigations have explored mother-infant vocal interactions [13] and the role of social calls in communicating a roosting bat's emotional and physiological state [14]. Last year, in a study that laid the groundwork for the current study, Wright *et al.* [15] showed for the first time that big brown bats also produce social calls during flight. Of particular interest was their discovery of a social call known as a 'frequency-modulated bout' — a call composed of three or four ultrasonic pulses that are longer in duration and lower in frequency than echolocation calls, and which are produced exclusively by males in a foraging context.

In the current study, Wright *et al.* [6] studied the function of frequency-modulated bouts by determining the precise context surrounding their

production and the effects that they have on other foraging bats. The study was not easy; it was complicated by the dark foraging environment, the rapid and erratic movements of foraging bats, and the inability of humans to hear the ultrasonic calls of interest. The authors overcame these obstacles by studying bats in a darkened flight room that was equipped with specialized recording equipment. Twin high-speed infrared-sensitive cameras mounted on adjacent sides of the flight room allowed the researchers to recreate the exact three-dimensional flight paths of foraging bats, while an array of ultrasound-sensitive microphones enabled them to triangulate the positions of callers and ascribe specific vocalizations to known individuals. This technological *tour-de-force* revealed moment-to-moment movements of bats relative to when vocalizations were produced, relative to the locations of other foraging bats, and relative to the location of a single prey item (a mealworm) tethered somewhere in the room. The researchers also manipulated the social context of each flight by flying male and female bats alone, with another bat of the same sex, or with another bat of the opposite sex.

The researchers conducted 1106 flight trials, and from these recorded 186 frequency-modulated bouts. Frequency-modulated bouts were produced exclusively by males, and only when a second bat was present in the flight room. More interesting was the fact that the emission of frequency-modulated bouts appeared to exert a strong and immediate effect on the behaviour of the other flying bat. During the 500 ms immediately following call emission, the distance between the two bats increased by an average of half a meter. Furthermore, if a bat was flying close to the prey item when the other bat emitted a frequency-modulated bout, it immediately moved away from the prey and appeared to abort its prey capture attempt. These results provide compelling evidence that frequency-modulated bouts repel rivals from both caller and prey. This, in turn, translates to an increase in the caller's foraging success; the individual that emitted more frequency-modulated bouts subsequently captured the prey

item almost two and a half times as often as the other individual.

These results provide strong evidence that frequency-modulated bouts repel rivals and thereby enhance prey capture, but they do not explain why these calls exert such an effect. Although this question will be the subject of many exciting studies in the future, the current study does provide valuable insight. By analyzing the acoustic structure of frequency-modulated bouts, the authors show that these vocalizations are individually distinctive, and that individual bats could, in theory, be identified reliably solely on the basis of their acoustic characteristics. If other bats use these cues to recognize callers, as has been shown in a wide range of other animal species [16], then they could adjust their behaviour according to their previous interactions with calling individuals. For example, recognizing a previously aggressive male could allow an individual to abandon its pursuit of a contested food item, and thus avoid any physical aggression that might otherwise ensue. Two lines of evidence support such a function. First, although male big brown bats often live alone, they do occasionally live with females or other males [17], making repeated interactions among known foragers possible. Second, some wild big brown bats patrol foraging grounds and use physical aggression to chase away competitors [18]. Taken together, this suggests that early recognition of aggressive individuals could be an adaptive trait that reduces the risk of injury to perceptive individuals.

The Wright *et al.* study [6] reveals a new level of complexity and functionality in what is already one of the most sophisticated vocal systems described. Yet the study also raises a host of interesting new questions. For example, what information do frequency-modulated bouts communicate? When two individuals meet, what determines which individual will call? Why do males call, but females do not? And, finally, how does the nervous system coordinate the multiple activities involved in foraging, thereby allowing bats to echolocate, fly, monitor competitors, emit social calls, and respond to social calls with split-second adjustments to foraging behaviour [19].

More generally, the study contributes to our understanding of how vocalizations mediate social interactions among foraging animals. Food-associated calls are produced by a wide range of species, but most appear to be cooperative, in that they increase the probability that the recipient approaches and consumes the food [20]. In contrast, the frequency-modulated bouts described here function to repel call recipients from food, suggesting that these signals have been shaped by very different selective forces.

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Neuroeconomics: A Formal Test of Dopamine's Role in Reinforcement Learning

Over the last two decades, dopamine and reinforcement learning have been increasingly linked. Using a novel, axiomatic approach, a recent study shows that dopamine meets the necessary and sufficient conditions required by the theory to encode a reward prediction error.

Eric E.J. DeWitt

Nearly two decades ago, researchers noticed that the activity of dopaminergic neurons bore a striking

resemblance to the reward prediction error signal predicted by reinforcement learning [1,2]. The notion of reinforcement learning was developed to unify and formalize decades of work