

Quick guide

Buzz pollination

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What is buzz pollination? Buzz pollination is a pollination syndrome in which bees use vibrations to extract pollen from flowers, incidentally fertilising them (Figure 1). The buzzing behaviour that some bees display on flowers to extract pollen has also been called ‘floral sonication’ due to the distinctive sound the vibrations produce. Buzz pollination is relatively widespread; flowers with buzz-specialised morphology are found across more than 20,000 species of flowering plants, including economically important crop species such as tomatoes, potatoes and kiwis, while flower buzzing has been observed in 74 genera comprising about 58% of bee species.

How do bees produce floral vibrations? When buzzing a flower, a bee holds onto the anther or other floral structure and produces vibrations using its thoracic muscles, while keeping the wings folded. These vibrations release pollen onto the bee’s body which she will later groom into place to carry back to the nest. To produce floral vibrations, bees use their flight muscles — specifically, the dorsal longitudinal and dorso-ventral muscles that fill the inside of the thorax and provide the power for flight. These muscles are asynchronous, meaning that the rate of muscle contraction is different from the rate of neural impulses received by the muscles. This disconnect between neuron firing rate and muscle contraction is due to stretch-activation — when one of the muscle sets contracts, it stretches the other set, triggering those latter muscles to contract. While insects with stretch-activated muscles can use neural impulses to control the overall power produced, this self-perpetuating cycle of muscle contractions allows the production of vibrations at much higher frequencies than would be possible without stretch activation. Floral vibration frequencies can exceed 300 Hz (cycles a second), with

some species approaching 400 Hz. The vibrations produced during floral vibrations are not exactly the same as those produced during flight. During flower-buzzing, bees vibrate their thorax at higher frequencies and higher amplitudes than during flight. These higher frequency vibrations appear to be partly due to the wings being folded over the abdomen, reducing the effect of drag and inertia on the vibrations, and partly due to differences in the pattern of neural impulses sent to the muscles. The properties of floral vibrations therefore depend on both the nervous system of the bees and biomechanics of the body.

Can all bees buzz flowers? No. Only about half of bee species can buzz flowers, including large carpenter bees as well as minute sweat bees. We do not currently know why some species

do not buzz flowers. On a mechanistic level, some bees might not be able to generate the forces required to release pollen, and so there is little point in buzzing flowers. Bumblebees and carpenter bees can produce buzzes with accelerations sufficient to release pollen from poricidal anthers, but honeybees (*Apis mellifera*) cannot reach the required acceleration. We still do not know why, on an evolutionary level, bee species differ in the buzzes they can produce.

What does a buzz-pollinated flower look like? Bees vibrate flowers of diverse floral morphologies (Figure 1). However, the vast majority of buzz-pollinated flowers conceal pollen inside anthers that open only through small pores or slits at their tip (poricidal anthers). The anthers of these species are enlarged, brightly coloured,



Figure 1. Examples of bees visiting buzz-pollinated flowers.

Clockwise from top left: Sweat bee (possibly *Augochlora* or *Augochloropsis*, Halictidae) on *Tibouchina* sp. (Melastomataceae) in Brazil; carpenter bee (*Xylocopa* sp.) on *Tibouchina* sp. in Brazil; unidentified bee on *Solanum houstonii* (Solanaceae) in Mexico; bumblebee (*Bombus* sp., Apidae) on *Senna alata* (Fabaceae). Photo credits: Douglas Moore (*Solanum houstonii*), Carlos Eduardo Pereira Nunes (*Senna alata*), and Mario Vallejo-Marín (*Tibouchina* sp.).

and presented prominently to the approaching visitors. The petals are often reflexed away from the anthers, which in some cases form a cone at the centre of the flower. There are more than 20,000 species of flowering plants with poricidal anthers, and these are mainly pollinated by bees that use floral vibrations to remove pollen. Classic examples of buzz-pollinated flowers with poricidal anthers include the 1,300 or so species of *Solanum* (including tomatoes, potatoes and aubergines) as well as most species in the tropical family Melastomataceae.

Other plant species have evolved different floral morphologies that conceal pollen and which require bee vibrations to remove it efficiently. For example, some *Pedicularis* spp. (Orobanchaceae) keep their anthers inside a tubular structure made of modified petals that release pollen only through a small terminal pore-like opening, while an unusual species of *Dalechampia* (Euphorbiaceae) in Madagascar has modified entire male flowers that take the functional role of a poricidal anther. Curiously, flowers of some species of Fabaceae combine poricidal anthers with highly modified, curved (*Senna* spp.) or even tubular petals (*Chamaecrista* sp.) that might act as extensions of the anther and facilitate pollen placement on bees.

How do buzz properties affect pollen release? Floral vibrations differ in properties such as frequency, duration and amplitude. These properties can affect how much pollen these buzzes release. In experiments in which flowers are vibrated and the pollen released measured, it has been found that high velocity and high acceleration buzzes released the most pollen. Bees can therefore release more pollen during floral vibrations by producing high velocity and acceleration vibrations. Indeed, the floral vibrations produced by buff-tailed bumblebees, *Bombus terrestris*, have higher velocities and accelerations than vibrations produced during flight or defence. The transmission of vibrations from the bee's thorax to the anthers is mediated by characteristics of the bee, the flower being vibrated, and the coupling between bee and flower.

Floral traits such as anther mass relative to mass of the bee, anther geometry and architecture, and its material properties might influence how bee vibrations translate into pollen release. Furthermore, the amount of pollen released for a given buzz can also change over time. Older virgin *Primula conjugens* (Primulaceae) flowers release more pollen than younger virgin flowers when buzzed at frequencies similar to those used by bees (less than 400 Hz). The ecological interaction between plants and bees through their biomechanics and behaviour make buzz pollination an excellent system to investigate the mechanical ecology of plant–animal interactions.

Can bees modify their buzzes? The buzz a bee produces differs among bee species and, in some cases, between larger and smaller members of the same species. In some species, individual bees can also modify the vibrations they generate, producing longer or shorter buzzes or buzzes at higher or lower frequencies depending on the plant species they are visiting. In other species, including other bumblebees, there is very little difference in the buzzes bees produce on different flowers, with most variation in vibration properties being caused by how plants transmit vibrations, rather than bees producing different vibrations. While foraging on a flower, bees can modify their buzzes based on how much pollen they are extracting. When a flower does not release pollen, bees may change the properties of their buzz, increasing the frequency or amplitude. Evidence for bees learning to produce buzzes with particular properties is mixed. Although bees seem to get better at buzzing flowers, collecting more pollen with experience, we are not sure why this is. Different studies have found changes in the frequency, duration, and amplitude of buzzes as bees gain experience, but attempts to train bees to buzz at higher or lower frequencies showed no signs of bees learning the 'best' frequency. Instead, bees continued to use the same heuristics they would use in other situations, increasing their buzzing frequency when flowers are not rewarding them with pollen.

Why does buzz pollination evolve?

The relationship between pollen-foraging bees and flowers goes back to the origins of bees in the early Cretaceous over 120 million years ago. While many plant species use nectar, oils, scents and other rewards to attract pollinators, buzz-pollinated plants are usually nectarless and almost exclusively rely on pollen. Pollen consumption leads to a potential conflict between plants and their pollinators. Poricidal anthers and other specialised floral morphologies of buzz-pollinated plants may have evolved to restrict pollen access by greedy and/or inefficient pollinators. These floral modifications may have in turn shaped the evolution of floral buzzing by bees. Flower buzzing has evolved over 45 times in bees and likely preceded the evolution of buzz-pollinated flowers as a method to improve pollen collection efficiency. However, restricting pollen access may have encouraged further evolution of this behaviour, resulting in an arms race between plants and bees and causing further evolution in buzz-pollinated flowers.

Is buzz pollination an evolutionary dead end?

For bees, buzzing is one of several behavioural tools to extract rewards. Many buzz-pollinating bees, like bumblebees (*Bombus* spp.), are generalists and will seek pollen on buzz-pollinated and non-buzz-pollinated flowers. Other bees rely more strongly on buzz-pollinated flowers. Several mining bees in the subfamily Oxinae strongly prefer buzz-pollinated flowers for pollen collection. As buzz-pollinated flowers are often nectarless, few bees can rely exclusively on buzz-pollinated plants, as they have to find nectar sources elsewhere. An exception might be those bees specialising in nectariferous buzz-pollinated flowers, such as the anthophorid (digger) bee *Habropoda laboriosa*, a blueberry specialist. It has yet to be seen if these bees possess specific adaptations for buzz pollination. For plants, the story may be slightly different as buzz-pollinated plants may rely heavily on visitation by buzzing bees for reproduction, leading to functional specialisation. It has been suggested that the morphological adaptations associated with buzz pollination

may have trapped these plants in an adaptive peak. Despite this, there are examples of plant species that have evolved other modes of pollination derived from buzz-pollinated ancestors. For example, a few species of Melastomataceae have evolved flowers with modified anthers that act as bellows to release pollen. When a pollinator collects floral perfumes (non-buzzing male orchid bees in *Solanum*) or remove the sugar-rich structures at the base of modified stamens (birds in Melastomataceae), the flexible anther is squeezed, producing a puff of air, which fires pollen onto the pollinator's body. Having lost their need for buzz pollinators, these flowers demonstrate the diversity of ways in which plants evolve to disperse their pollen.

Where can I find out more?

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Primer

Model-based decision making and model-free learning

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Free will is anything but free. With it comes the onus of choice: not only what to do, but which inner voice to listen to — our ‘automatic’ response system, which some consider ‘impulsive’ or ‘irrational’, or our supposedly more rational deliberative one. Rather than a devil and angel sitting on our shoulders, research suggests that we have two decision-making systems residing in the brain, in our basal ganglia. Neither system is the devil and neither is irrational. They both have our best interests at heart and aim to suggest the best course of action calculated through rational algorithms. However, the algorithms they use are qualitatively different and do not always agree on which action is optimal. The rivalry between habitual, fast action and deliberative, purposeful action is an ongoing one.

In this primer, we first expand on the theoretical and computational basis of each of the two systems and their neural substrates. Given the evidence that the two systems work in tandem, we then discuss how the brain arbitrates between them by asking what are the conditions under which each system is preferentially used. Finally, we discuss a task developed to test the theoretical assumptions about the two modes of decision making in humans.

Goal-directed versus habitual behavior

The idea of two systems of control, one dependent on deliberation and one based on automatic reactions, has roots in the psychological literature on instrumental conditioning and the differentiation between goal-directed and habitual behavior. In instrumental conditioning, animals learn which action (or series of actions) will bring about a desired outcome, for example rats learning to press a lever for food reward. Outcomes that increase the performance of an action are ‘reinforcers’ — whether appetitive, in

the rat example food increasing lever-pressing, or aversive, as when a shock increases escape behavior.

What do animals learn in instrumental conditioning? Early theorists suggested two main alternatives: according to Edward Thorndike, the core of instrumental learning is the formation of associations between stimuli and responses (‘S–R’ learning), with the reinforcer ‘stamping in’ these associations, but not being part of the learned construct. In contrast with this behaviorist view, Edward Tolman, foreman of the cognitive revolution, argued that animals learn more elaborate cognitive maps. In these, the learned association is between actions and their outcomes, broadly construed (‘A→O’ learning), and the association is predicated on their causal contingency (which we denote by →).

As highlighted by Robert Rescorla, Ruth Colwill, Anthony Dickinson and Bernard Balleine, these competing models make contradictory predictions: Tolman’s A→O model suggests that behavior should be sensitive to two things: changes in the value of the outcome, for example, if the outcome is no longer desired due to satiety, the rat will decrease its rate of pressing; and changes in the contingency between the action and the outcome, for example, if the action no longer leads to the outcome, the rat will cease to perform the action.

Thorndike’s theory, on the other hand, predicts that learned actions will be impervious to such environmental (or internal) changes, as once they are stamped in, they will not be ‘stamped out’ except by aversive outcomes. Indeed, not all decisions to press a lever are created equal: for an animal to make a deliberative, purposeful choice, it must choose the action because it knows it will result in a food pellet, and the food pellet is desirable to it (as in Tolman’s model). However, as per Thorndike, this is not the only reason an animal may choose to press a lever.

What do animals do when the environment changes in such ways? It depends. In particular, early findings showed that rats that were trained extensively to press the lever indeed persisted in pressing for an undesirable outcome, as predicted by stimulus–response learning. However, rats that were only trained for a moderate

