BIOINSPIRED ROBOTS

Pollen tube navigation can inspire microrobot design

Tetsuya Higashiyama

Modeling of microrobots can be inspired by prominent features of flowering plant pollen tubes and their directional control to deliver cargo to distant targets.

Tip growth of cells occurs in a variety of organisms, including the hyphae of fungi, filaments of algae, and root hairs and pollen tubes of flowering plants. Polarized growth via localized biosynthesis at the tip is a unique mode of cell growth that contributes to colony expansion, nutrient acquisition, and cargo delivery. Thus, tip growth could inspire researchers in the design of new bioinspired robots. Pollen tubes of flowering plants are a particularly intriguing model for microrobots due to their unique properties, including extremely rapid cell growth and precise navigation.

When a pollen grain (typically 20 to 60 μm in diameter) lands on the tip of a flower pistil, a tubular cell called the pollen tube (around 10 μm in diameter) emerges from the grain. The pollen tube must then travel anywhere from 1 mm to 30 cm, depending on the plant species, to the egg cell embedded deep in the pistil. The function of the pollen tube is to deliver sperm cells. Unlike animals, the sperm cell of flowering plants is nonmotile and engulfed by the tube cell. The small sperm cell is transported with the tube cell nucleus and other cytosolic components to the tip of the pollen tube. Pollen tubes of flowering plants grow quickly—typically 500 to 2500 μm/hour and over 10,000 μm/hour in some species (*1*)—facilitating rapid seed formation even in relatively dry conditions and thus contributing to the evolutionary success of flowering plants.

The pollen tube grows at its tip due to localized active secretion that provides the cellular membrane and wall materials for growth (*2*). Pollen tube cells are metabolically active and express genes for biosynthesis and secretion, but this is insufficient for pollen tube growth. Female tissues additionally provide materials, such as sugars, lipids, ions, small compounds, and water, so that pollen tubes can grow to a length 100 to 10,000 times the original diameter of the pollen grain. Pollen tubes are occupied by vacuoles, water-containing organelles, and long pollen tube cells are segmented by unique cell walls called callose plugs that prevent the backflow of the sperm cell and cytoplasmic components located at the tip.

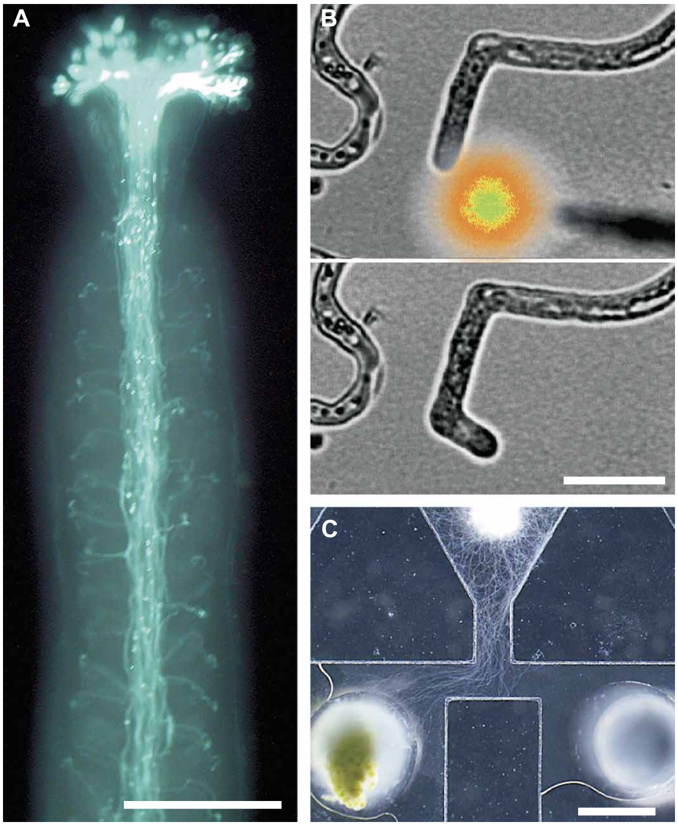

Fig. 1. Pollen tube guidance in flowering plants. (**A**) Pollen tube guidance in *Arabidopsis thaliana*. Pollen tubes in the pistil were stained with aniline blue. Note the one-to-one guidance. Scale bar, 500 μm. [Image credit: M. M. Kanaoka, Nagoya University.] (**B**) A *Torenia fournieri* pollen tube attracted to LURE peptides (orange). The image in the bottom panel was acquired about 6 min after that in the top panel. Scale bar, 20 μm. [Image credit: Reproduced from (*4*).] (**C**) Long-distance attraction of *T. fournieri* pollen tubes to ovules in a microfluidic channel. Several pollen tubes originating from the top can be seen turning left, toward green ovules. Scale bar, 1 mm. [Image credit: Reproduced from (*5*).]

To achieve successful fertilization for seed production, female tissues along the tube path control the growth direction of the pollen tube. This process, known as pollen tube guidance (Fig. 1A), requires both chemotropic and mechanical guidance to maintain control (*3*). In the style (a long and thin component of the pistil) of the lily, pollen tube guidance is mechanical, similar to a one-way tunnel (*3*). The ovule tissue (the seed tissue before fertilization) then attracts pollen tubes chemotropically. After a long, intensive search for 140 years, LURE peptides were the first attractants to be discovered and identified in *Torenia fournieri*, the wishbone flower (Fig. 1B) (*4*). LUREs are cysteine-rich peptides made up of about 70 amino acids. LUREs are secreted from two cells on the side of the egg cell and are responsible for the final step of guidance, which is very precise and short in distance (~200 μm; movie S1). Ovules are likely to produce other long-distance attractants that attract pollen tubes roughly (Fig. 1C) (*5*), although the responsible molecules have yet to be identified.

The control of pollen tube growth direction by attractant peptides is an intricate process. It has recently been reported that LURE peptide receptors are localized at the cell membranes of the tip of the pollen tube in the model plant species *Arabidopsis* (*6*, *7*). The cell surface receptor heteromer MDIS1-MIK and the pollen-specific receptor-like

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kinase 6 (PRK6) are receptor-like kinases with a single transmembrane domain. It has been proposed that they detect LURE peptides outside the cell and transduce the signal inside the cell to control the exit sites of secretory vesicles (*8*). Tip localization suggests that receptors are recycled by both endocytosis at the subapical zone and resecretion at the apical zone. Live imaging has captured the asymmetric localization of PRK6 toward the side of the cell membrane on which LURE was administered (*7*). PRK6 interacts with core pollen tube growth machinery, suggesting that these dynamics are important for directional control (*7*).

A prominent feature of pollen tube guidance is the one-to-one ratio of pollen tube to ovule. This relationship is obvious in a pistil with multiple ovules; in the genus *Arabidopsis*, each of the 50 ovules in a pistil attracts only one pollen tube (Fig. 1A). By contrast, in animals, multiple sperms may reach an egg. The mechanism behind this one-to-one guidance of flowering plants remains unknown, but it has been proposed that a repellant molecule deters the second pollen tube from approaching (*3*, *8*). Live-cell imaging of pollen tube guidance in the deep pistil tissue may clarify the mechanism. Irreversible cessation of pollen tube attraction after fertilization also plays a role in one-to-one guidance [polytubey block (*8*)].

Another prominent feature of pollen tube guidance is the species specificity of ovular attraction, which contributes to reproductive barriers between different species. When the genes of ovular attractant peptides, such as LURE in *Arabidopsis thaliana* or EGG APPARATUS 1 (EA1) in maize, were introduced to other distantly related plant species, pollen tubes of *A. thaliana* or maize were attracted to such transgenic species by overcoming barriers (*8*). Similar breakdown of barriers was demonstrated by introducing the receptors PRK6 and MDIS1 to other plant species (*6*, *7*). Therefore, attractant-receptor pairs can be used as lock-and-key mechanisms in pollen tube guidance between specific partners. Solving cocrystal structures of LURE and their receptors are of interest to understand the lock-and-key mechanism.

Pollen tube–inspired microrobots may provide a unique opportunity to precisely transport cargo to distant and specific targets. Understanding the mechanisms behind pollen tube guidance will contribute to the development of robot navigation systems and vice versa. Recently, it was discovered that the pollen tube delivers not only the sperm cell but also unidentified bioactive molecules for seed development (*9*). Additionally, pollen tubes, as well as their nuclei and sperm cells, were shown to pass through a 1-μm gap (*10*). Pollen tubes serve as unique and interesting inspiration for bioinspired microrobots.

SUPPLEMENTARY MATERIALS

robotics.sciencemag.org/cgi/content/full/2/8/eaao1891/DC1
Movie S1. Pollen tube attraction to the ovule in *Torenia fournieri*.

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