Physarum

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***What is** Physarum?* *Physarum*, or more precisely *Physarum polycephalum*, is an acellular slime mold, or myxogastrid. Myxogastrids are closely related to the cellular slime molds, or dictyostelids, including the well known *Dictyostelium discoideum*. *Physarum* is more distantly related to the protostelids (together these groups are discussed as the eumycetozoans, or 'true' slime molds) and very distantly related to other species also called slime molds, for example acrasids.

Why 'acellular'? *Physarum* first grows as single-celled amoebae, but the amoebae fuse, and the organism loses its 'cellular' makeup (Figure 1). As the organism continues to grow, nuclei divide without cell division. The resulting bag of nuclei is called a 'coenocyte' or 'plasmodium'. It is covered in a layer of glycoprotein gel, giving it a slimy appearance. The plasmodium forms a tubular network, and as it moves, the network is reshaped and adapted to the environmental stimuli the tubes encounter. Cytoplasm streams through the network, and the streams periodically change direction. Slime molds are typically found in moist forest environments and probably feed on microbes growing in leaf litter, bark, mushrooms and other substrates. Here, individuals can be very large, even up to several feet in diameter. Given the right conditions (depleted food and exposure to light), a plasmodium will develop small, stalked fruiting bodies resembling typical fungal molds. These fruiting bodies contain haploid spores, each of which hatch a single mononucleate amoeba, completing the basic life cycle.

How long has** Physarum **been used as a model in biology? The groundwork for research on *Physarum* was laid by H.P. Rusch and colleagues, and during its heyday in the late 1970s to early 1980s, there were about 60 *Physarum* papers per year. Research ranged around three topics: differentiation and development, the cell cycle, and motility. Its complex, potentially reversible life cycle made the slime mold a rich model for developmental biologists. Because *Physarum's* plasmodium has a naturally synchronous nuclear division, with thousands of nuclei dividing every 8–10 hours, the organism is ideal for cell cycle experiments. Moreover, the slime mold moves using an acto-myosin cytoskeletal system similar to systems used by animals, and is a widely relevant model for motility. The last decade has been witness to a surge of interest in the self-organizing behaviors of *Physarum*'s tubular network and the use of these behaviors to solve complex engineering problems.

Why is** Physarum **sometimes described as 'intelligent'? Obviously, *Physarum* doesn't have a brain, but its emergent behaviors are more complex than the localized decisions of its parts, and the slime mold can solve complicated problems. For example, it can find the shortest path through a maze. The network can connect different resources and allocate biomass proportionally to derive an optimal diet. Networks transport substrates efficiently, but also are sufficiently redundant to be robust to the destruction of tubes. As these examples illustrate, the organism makes behavioral decisions based on aggregate knowledge of each of its parts. *Physarum* must have mechanisms to move information along its tubes, and sum diverse sources of information into a behavior.

What enables communication across an individual? Information in the form of molecular signals and nutrient concentrations can be rapidly sent around the tubular network using the streaming cytoplasm. Cytoplasmic flows change direction about every 100 seconds, and can reach speeds of up to 1 mm/s. Cross-sectional, acto-myosin based contractions of the tubes drive flows. Contractions are organized in a peristaltic wave to create coordinated flows optimal for transport. The length of the peristaltic wave is actively matched to the organism's size, so that points of zero flow velocity are eliminated. With these flows signaling molecules or nutrients are rapidly distributed throughout the organism. The net transport of cytoplasm from one end of the network to the other is also the basis for movement by the slime mold. Cytoplasmic flows not only move signals, they also move the organism as a whole.
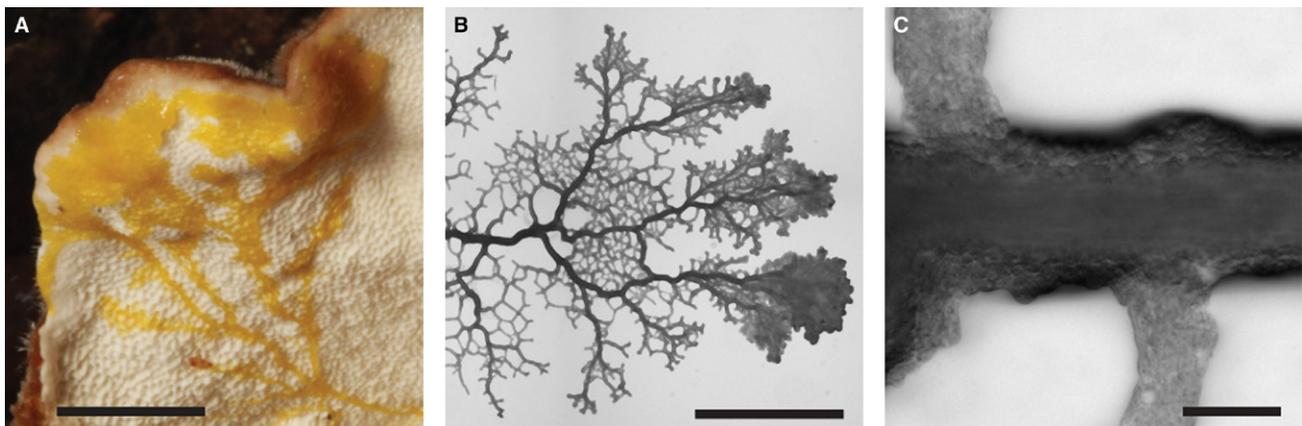
Figure 1. *Physarum polycephalum.*
(A) The slime mold is typically found on organic substrates in humid, shady habitats. Scale bar ~0.5 cm. (B) Bright field microscopy image showing the tubular network of the organism with more fan-like structures at the growing front (to the right). Scale bar 0.5 cm. (C) The cytoplasm streams within the network's tubes. Scale bar 100 µm.

How are stimuli parsed to enable behavior? To transition from sending signals around to coordinating a behavior, *Physarum* needs to somehow store and process information about stimuli. Stimuli are commonly encountered at the edge of an individual's network, where flows become vanishingly small. Any molecular signal triggered by a stimulus at the edge will therefore not be homogenized throughout the network. Instead, the organism may use the resulting local concentration gradient to 'remember' the location of a stimulus. However, the idea of memory in a slime mold is speculative and how information is processed within the organism remains to be discovered.

Are the behaviors of Physarum *unique?* No. Although *Physarum* is not a fungus, fungi also grow as networks and many species forage for scarce and heterogeneously distributed resources, for example fallen wood. Both slime molds and fungi are major components of the biodiversity of ecosystems. Although both groups are of obvious ecological relevance, the behaviors of slime molds and fungi are also intrinsically fascinating. Integrated behaviors require communication and decisions. The mechanisms used by *Physarum* to coordinate growth and make choices will almost certainly inform our understanding of other species' behaviors.

Where can I find out more?

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Ants use a predictive mechanism to compensate for passive displacements by wind

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Insect navigation is a fruitful system for analysing the ingenious and economical mechanisms that can underlie complex behaviour [1]. Past work has highlighted unsuspected navigational abilities in ants and bees, such as accurate path integration, long distance route following or homing from novel locations [2]. Here we report that ants can deal with one of the greatest challenges for any navigator: uncontrolled passive displacements. Foraging ants were blown by a jet of air over 3 meters into a dark pit. When subsequently released at windless unfamiliar locations, ants headed in the compass direction opposite to the one they had been blown away, thus functionally increasing their chance of returning to familiar areas. Ants do not appear to collect directional information during the actual passive displacement, but beforehand, while clutching the ground to resist the wind. During that time window, ants compute and store the compass direction of the wind. This is achieved by integrating the egocentric perception of the wind direction relative to their current body-axis with celestial compass information from their eyes.

Melophorus bagoti ants forage individually during the hot central Australian summer days, seeking seeds and roasted insects while ground temperatures rise above 50°C. Each forager develops its own idiosyncratic visually-guided route that meanders between buffelgrass tussocks [3]. Thermal turbulences due to solar heating of the ground create frequent wind gusts and it is not rare to see ants getting blown away from their familiar route. The displacement may only be a few meters, but for an ant this corresponds to hundreds of body lengths of violent tumbling through dust and vegetation, making it virtually impossible to determine and integrate self-motion during the displacement.

We investigated how *M. bagoti* copes with such passive displacements by simulating wind gusts using a leaf blower. Two small piles of cookie crumbs were placed 10 cm north and south of the nest entrance (Figure 1A, grey dots). As soon as an individual ant emerged from the nest and picked up a cookie crumb, a horizontal wind was generated along the ground, blowing the ant 3 m either east or west towards a vertical barrier designed to stop the passive displacement. Displaced ants would then fall into a pit, then be transported in darkness and released in windless conditions at a distant unfamiliar location (see Supplemental Information available on-line with this issue).

A control group of ants that did not get blown away showed the characteristic undirected headings of a systematic search (Figure 1H), confirming that the scenery at the release point did not provide any directional information. In contrast, ants that had been blown away showed directed headings. They walked in the compass direction opposite to the blast of air they had experienced: ants blown eastwards headed westwards and vice versa (Figure 1B). Two replications of this condition — with ants from another nest and at another release location — gave similar results (Figure 1C,D). This indicates that *M. bagoti* ants can somehow collect information about the compass direction in which they have been blown away.

Given how quick and turbulent the passive displacement is (see Supplemental Movie S2), how can ants derive such directional information? We first suspected a role for the ocelli, the three small single-lensed eyes on top of the ant's head, which mediate fast sensing of body rotation in some flying insects [4] and extract celestial compass information in ants [5]. We repeated the experiment