to maintain ring association with the membrane specifically during contraction? Since considerable stress is exerted on the membrane during furrowing [10], Inn1 might alter plasma membrane properties, like viscosity or curvature, to promote membrane deformation and to stabilize membrane–ring interactions specifically during furrow ingression. Insertion of the Inn1 C2 domain into the lipid bilayer could have such an effect on the cleavage furrow. In a related case, insertion of the C2 domain of the human vesicle fusion protein synaptotagmin [11] leads to increased membrane curvature. Is regulation of membrane curvature important for furrow ingression? Further studies aimed at characterizing the interaction of Inn1 with membranes should help to answer this question.

If Inn1 were indeed actively involved in membrane remodeling, it would be interesting to address whether it also acts in abscission, when the plasma membrane undergoes the dramatic transition from continuous lipid bilayer into two distinct membranes. This is a poorly understood process in which ring disassembly and vesicle fusion events may play an important role [2,12]. In this context, the observation by Sanchez-Diaz *et al.* [5] that actomyosin ring disassembly is delayed in Inn1-depleted cells is intriguing and could indicate that ring disassembly and abscission are coordinated by a membrane-bound factor, perhaps Inn1 itself.

This recent work [5] identifies Inn1 as the first factor known to link the actomyosin ring to plasma membrane ingression. Although animal cells have no obvious Inn1 homologues, C2 domains are ubiquitous in eukaryotes. It is likely that C2-containing proteins will turn out to be important players in cytokinesis in animal cells. At the last count, more than 270 human proteins were annotated as possessing C2 domains, many of them of unknown function. The hunt is on.

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ETH Zurich, Institute of Biochemistry, HPM D14, Schafmattstrasse 18, 8093 Zürich, Switzerland.
E-mail: manuel.mendoza@bc.biol.ethz.ch, yves.barral@bc.biol.ethz.ch

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Behavioural Genetics: Worms Seek That Old Beetle Smell

Some nematodes eavesdrop on pheromonal signals to sniff out their elderly beetle hosts. This turns out to be yet another behaviour regulated by cGMP/PKG signalling.

Marla B. Sokolowski[1] and Mark J. Fitzpatrick[2]

Like vultures of the undergrowth, some nematodes lurk in the soil searching for over-the-hill hosts. They climb aboard an unsuspecting beetle and enter a hibernation-like state until the host dies. Because the nematodes do not appear to harm the living host, they are not parasites; rather, upon the death of the host, the nematodes reawaken to feed on the microorganisms found in the carcass. Fascinating new investigations of the chemosensory aspects of this necromenic lifestyle are described in two recent papers by Hong *et al.* [1,2].

Necromeny in *Pristionchus* nematodes is a very recent discovery [3,4]. These worms exhibit chemoattraction to insect sex pheromones as well as to extracts from plant compounds [1]. They have evolved to intercept the chemical communication system of their insect hosts. In one scenario, the scarab beetle host lives about three years as a larva and pupa, but only three weeks as a feeding adult. The shorter-lived nematodes have evolved to specifically recognize the older feeding beetles, their preferred targets, and Hong *et al.* [1] show that beetle chemosensory cues provide the necessary information. The species *P. maupasi* is most attracted to a cocktail from late-stage feeding beetles, which move repeatedly between soil and foliage, and are generally only weeks from death. In this case, the pheromone and plant volatiles associated with feeding beetles act synergistically to increase chemoattraction of this nematode species. This has two interesting consequences: first, the use of sex pheromones as an attractant ensures that the worms infect the proper species, and only the adults so that they avoid getting 'trapped' for years on a larva or pupa; and second, the synergistic attractant effects of the plant volatiles may help the worms identify hosts who have made more feeding forays, and are therefore older and closer to death.

The species *P. pacificus* (Figure 1) associates with the oriental beetle *Exomala/Anomala orientalis* [3] and is attracted to its pheromone (Z)-7-tetradecen-2-one (ZTDO) [2], as well as to the moth pheromone (E)-11-tetradecenyl acetate (ETDA) [2,5]. Hong *et al.* [2] show that significant differences in attraction to these pheromones are found in nineteen strains representive of the currently known geographic distribution of *P. pacificus*. The largest difference in chemoattraction is found between the high attraction Washington (WA) strain and the low attraction California (CA) strain. This provided the raw material to embark on a genetic analysis of natural variation in this intriguing necromenic lifestyle [2].

Figure 1. Scanning electron microscopy image of a young *Pristionchus pacificus* hermaphrodite.

Image courtesy Ray Hong and Juergen Berger, Max Planck Institute for Developmental Biology.

Several step-wise approaches were needed to identify the gene(s) associated with the differences in ETDA pheromone chemoattraction between the WA and CA strains. Recombination mapping localized the behavioral differences to a small region on the fourth pair of *P. pacificus* chromosomes [2]. Among the genes in this region is the *P. pacificus* ortholog of the *Caenorhabditis elegans* gene *egl-4*, named *Ppa-egl-4*. This gene is an exciting candidate for involvement in pheromone chemoattraction, as it encodes a cyclic GMP-dependent protein kinase (PKG), an enzyme which is known to play a role in olfactory and food search behaviours in *C. elegans* [6,7] and in food-related behaviours in *Drosophila* [8,9] and social insects [10,11] .

Evidence that *Ppa-egl-4* is involved in pheromone chemoattraction was obtained using a number of approaches. From a series of repeated backcrosses, Hong *et al.* [2] generated lines that contained either the WA *Ppa-egl-4* allele in a CA genetic background or the CA *Ppa-egl-4* allele in a WA background. The behaviour of these lines supported the hypothesis that the differences in chemoattraction to ETDA between the WA and CA strains was largely, but not completely, attributable to natural variation in *Ppa-egl-4* [2]. This suggested that *Ppa-egl-4* had a major effect on this naturally occurring behaviour but other smaller effect genes were also likely involved.

This pattern of genetic architecture parallels findings for the *Drosophila foraging* gene, the ortholog of *egl-4*, polymorphisms of which are responsible for the naturally occurring rover and sitter behavioural variants of the fruitfly. No consistent differences in DNA sequence were found between the *Ppa-egl-4* alleles of the various ETDA sensitive and insensitive strains [2]. This suggests that critical DNA polymorphisms may reside in yet undescribed regulatory regions of *Ppa-egl-4* or there may be independent DNA polymorphisms that explain the differences between the various ETDA sensitive and insensitive strains. Whether or not natural variation in genes important for behaviour should be expected to localize to the same coding or regulatory sequence in many populations sharing the same behavioural polymorphisms is currently unknown.

Both pharmacological and genetic manipulations were used to further demonstrate the link between *egl-4* and pheromone chemoattraction. CA worms fed 8-Br-cGMP, a known activator of PKG, showed increased *Ppa-egl-4* mRNA expression characteristic of the WA strain [2]. The 8-Br-cGMP treatments did not affect transcript levels in the WA strain. However, because 8-BrR-cGMP activates the pool of available PKGs to alter behaviour, the activator is expected to directly affect PKG activity and not mRNA level, unless a feedback loop which acts on *egl-4* mRNA levels exists. Further demonstration of a role for *Ppa-egl-4* in ETDA chemoattraction was based on attraction to ETDA being abolished in a null mutant of *Ppa-egl-4* exposed to exogenous cGMP [2].

To investigate whether these results could be generalized to the beetle pheromone ZTDO, which also differentially attracts WA and CA strains, worms lacking *Ppa-egl-4* were fed cGMP and their response to ZTDO was assessed. Although cGMP treatment increased wild-type worm attraction to ZTDO, the null allele of *Ppa-egl-4* did not alter this chemoattraction. This suggests that *Ppa-egl-4*'s role in chemotaxis may be specific to ETDA. These findings provide important insights into natural genetic variation in pheromone attraction and the possible specificity of the cGMP-PKG pathway. Hong *et al.* [2] suggest that distinct genetic factors are involved in the attraction of these necromenic nematodes to each of these pheromones. Necromenic nematodes are found with beetles that produce ZTDO and may also be associated with *Helicoverpa* moths that produce ETDA (Ray Hong, personal communication).

PKG encoded by *egl-4* in nematodes — and by the *foraging* gene in insects — is an important modulator of numerous behavioural phenotypes. In addition to its newly described role in necromenic host chemoattraction [2] along with olfaction [6,7] and food searching [8–12] discussed above, PKG affects egg-laying [13], body size [12,14], lifespan [14], sleep [15,16], dauer formation [6], learning and memory [17,18], energy homeostasis and food intake [8], sucrose responsiveness [19], and neural protection from thermal stress [20]. These illustrate only a subset of the many pleiotropic effects associated with PKG in different species. PKG appears to be a conserved molecular modulator of behaviour. While these pleiotropies sometimes present obstacles to our research, they are arguably the most interesting aspects of the work on PKG. Several questions challenge researchers working on both the evolution and mechanisms of this system: Why PKG? What is special about this particular enzyme or its gene? Is it a keystone molecule with important regulatory connections to many gene and molecular networks? Is this unique or are there other such molecular modulators of behaviour? How can this PKG sustain such a high level of pleiotropy and just as importantly, how can it sustain variability when many of the associated phenotypes have vital implications on fitness? The continued emphasis and success of integrative approaches within and between disciplines and study organisms will be critical as we overcome these challenges to gain an understanding of the complex relationships between genes and their phenotypic effects.

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[1]Department of Biology, University of Toronto Mississauga, Mississauga Ontario, L5L 1C6, Canada. [2]Integrative Behaviour & Neuroscience Group, Department of Biological Sciences, University of Toronto Scarborough, Toronto Ontario, M1C 1A4, Canada.
E-mail: marla.sokolowski@utoronto.ca, mark.fitzpatrick@utoronto.ca

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Animal Navigation: The Evolution of Magnetic Orientation

Animals have several types of magnetic organ, often separately specialized for determining direction versus location. Recent results offer hints about how these once-unimaginable detectors may have evolved.

James L. Gould

Few abilities have captured both the popular and professional imagination in quite the way the magnetic sense has. The Earth's magnetic field exerts a mysterious and invisible force which somehow passes through water and tissue to gently rotate compass needles toward a distant and unseen pole. By 1900 'magnetic intuition' and other imagined byproducts of this pervasive energy field were regularly invoked to account for a variety of (sometimes real) phenomena. However, the possibility of a magnetic sense in animals soon suffered from the skeptical backlash that accompanied the Clever Hans debacle (a trained horse that could apparently do arithmetic — it turned out the trainer was providing inadvertant clues to the answer in his body language).

It's a reflection of the sea change in attitudes that just thirty years after the first magnetic organs were discovered, most researchers (with notable exceptions [1]) not only take the internal compass for granted, but also believe that the magnetic sense in some animals can detect fields hundreds or thousands of times smaller than what is needed for merely judging direction. Such sensitivity allows animals not just to find north, but to actually compute map coördinates with a resolution of a few kilometers (or, quite possible, much better) [2,3]. How do animals do it — and where did this ability come from? A recent *Current* Biology paper by Stapput *et al.* [4] sheds light on both questions, suggesting that a more specialized light-dependent compass has evolved at least twice to supplement and at least partially replace what would seem to have been a perfectly good magnetite-based strategy.

There are three basic tricks for measuring the direction and strength of the earth's magnetic field [2]. All depend on the behavior of electrons: when a charged particle moves, it creates a minute magnetic field. This can be conventional linear movement through a conductor, or merely the natural spin all electrons possess. The simplest strategy (at least to the human imagination) is permanent magnetism: a substance like magnetite retains a permanent field; this field interacts with the earth's field, creating a pressure to align the two; this