

most remarkable finding because of the complexity of the circuitry involved in generating direction selectivity. The simplest way of endowing tectal neurons with direction selectivity would be for specialised direction-selective retinal ganglion cells to target tectal neurons; binocular target cells would then require input from ganglion cells with matched preferences in the two eyes. But this is not the way it is done. Ramdya and Engert [3] employed an apparent motion stimulus — a dot jumping from one position to a nearby one without actually moving there smoothly — to which direction-selective retinal ganglion cells do not respond, and still recorded direction-selective tectal responses. Significantly, binocular tectal neurons even responded when dots were shown in nearby retinal positions but to different eyes (Figure 1C). This clearly indicates that inputs from the ipsilateral eye are functionally fully integrated into the intrinsic circuitry of the rewired tectum. Tectal direction selectivity is likely to be generated by a temporally asymmetric inhibitory input. Local disinhibition by means of bicuculline, an antagonist of γ -amino butyric acid (GABA), the principal inhibitory neurotransmitter in the tectum, largely abolished tectal direction selectivity.

Taken together, the findings of Ramdy and Engert [3] suggest that precise integration of binocular signals, of the sort observed in the mammalian primary visual cortex, is not that special after all. It appears that convergence of retinotopically matched afferents from the two eyes is sufficient for the requisite binocular circuitry to develop spontaneously. The setting-up of this circuitry does not depend on any visual input but is most probably directed by gradients of guidance molecules such as ephrins [9]. This mechanism is so robust that even profound interventions like the rotation of one eye do not disturb it [10,11]. On the other hand, visual experience is required for the maturation and maintenance of binocularity [8,12].

There is, however, one significant difference between what is a functional match between two laterally positioned eyes in the zebrafish and two frontally positioned eyes in a cat or monkey: matching directions of motion in the

two eyes are head-to-tail or *vice versa* in the fish, but left to right or right to left in an animal with true stereoscopic vision (Figure 1D). In order to achieve functionally meaningful alignment of binocular inputs in the mammalian superior colliculus, retinal guidance molecules would therefore have to exhibit radial, rather than nasotemporal, gradients [13]. Evidence for such gradients has indeed recently been described for the human embryonic retina [14].

It seems clear that the development of topographically precisely matched binocular afferentation in visual brain areas is necessary for the evolution of stereopsis, but it is not sufficient. Equally, binocular convergence can in many cases result in interdigitating patterns of afferentation, such as ocular dominance columns, but it need not do so in order for stereopsis to develop, as is evidenced by many species of New World monkeys with poor segregation of left- and right-eye inputs in the primary visual cortex [15]. Molecular guidance cues appear to provide the framework within which visual experience fine-tunes the binocular circuitry underlying stereopsis.

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Reproductive Evolution: Symptom of a Selfing Syndrome

In the nematode *Caenorhabditis elegans*, a single gene (*plg-1*) encodes the dominant protein found in mating plugs — a means of inhibiting multiple matings. Naturally occurring loss of *plg-1* function results in males that fail to deposit mating plugs — a manifestation of relaxed sexual selection since the evolution of self-fertilization in this species.

Asher D. Cutter

In many animal groups, such as nematodes, insects, arachnids, reptiles, and mammals [1], copulatory plugs are formed in the female sexual tract after mating. These plugs are

mostly male-induced and can serve a number of conceivable functions: Plugs have been proposed to aid in reducing sperm loss or ejection after insemination. Alternatively, mating plugs might incapacitate the sperm deposited by previous males, act

to stimulate female reproductive physiology, or be sufficiently large that they provide an edible semen-derived nuptial gift, a so-called 'spermatophylax' [1]. Finally, copulatory plugs can inhibit subsequent males' attempts at mating or insemination — a physical, rather than behavioral, form of mate guarding. It should also be noted that in some organisms it is not the male, but the female, that produces a mating plug after copulation. Moreover, females can sabotage or inhibit plug deposition by males, and plugs could be advantageous to females as well as to males by facilitating female choice of sperm, avoiding additional costly matings, preventing infection, or supplying a source of nutrition [1].

Hermaphrodite *Caenorhabditis elegans* worms mated to some males invariably leave with a gelatinous blob stuck to their genitalia, but males of many natural isolates as well as the standard laboratory strain Bristol N2 do not deposit such a copulatory plug upon mating. Much like in other animals, when a plug is present, subsequent male mating attempts are inhibited [2,3]. Over 10 years ago, Jonathan Hodgkin and Tabitha Doniach [4] mapped this naturally dimorphic trait to a single locus, *plg-1*, but its molecular identity remained a mystery. Michael Palopoli, Matthew Rockman and colleagues [3] have now closed this gap. In a recent study, they characterized the molecular basis of copulatory plug formation in *C. elegans*, as well as the cause of some male's inability to deposit a plug. Using a combination of mapping approaches, they focused on a narrow region of chromosome III, in which they detected a length variant due to a retrotransposon insertion in the N2 strain that interrupts the coding sequence of a novel, previously unannotated mucin gene. Further experiments demonstrated conclusively that the mucin gene corresponds to *plg-1*, and that its protein product is the dominant constituent of the gelatinous mass comprising the copulatory plug. Like the major copulatory plug protein in *Drosophila melanogaster* (PEB-me), PLG-1 from *C. elegans* is characterized by extensive peptide repeats that are rich in proline and serine [5]. Semen-coagulating proteins of mammals also are repeat-rich, facilitating cross-linking during plug

formation [6]. Despite these emerging shared molecular properties of plug proteins, many open questions remain relating to whether diverse groups of organisms make use of homologous proteins in their plugs, whether plug proteins interact with or act as a substrate for the activity of other proteins, and how dynamic plug protein molecular evolution is in general.

The work of Palopoli, Rockman and colleagues [3] revealed that retrotransposon presence or absence at the *plg-1* locus is the cause of naturally occurring variation in whether or not *C. elegans* males deposit a mating plug. Dissection of this phenotypic dimorphism is enlightening for at least three reasons: First, it provides yet another impressive example of the role that transposable elements can have in phenotypic evolution [7]. Second, this case study suggests that genes with limited pleiotropy — such as *plg-1* — might represent stronger candidates for rapid phenotypic evolution than loci that influence many traits, in line with theory [8]. Third, the high selfing rate in *C. elegans* [9,10] is implicated as a key facilitating factor for the abundance of strains that have lost this mating-related trait, due to a single mutation event [3,4]. This trait-loss parallels the plant 'selfing syndrome'.

The selfing syndrome of flowering plants — self-fertilizing taxa are characterized by small and inconspicuous flowers, little pollen investment, absence of nectar reward, and reductions in other traits that encourage cross-fertilization [11] — is age-old in the botanical literature, with early work recognized by Charles Darwin in his seminal book on plant reproduction [12]. The diminution of such reproductive traits is due partly to relaxed selection for their maintenance, following the origin of self-fertility, and partly to selection favoring those characters that ensure self-fertilization. In animals, the evolution of mating-related traits in self-fertilizers is no exception.

Comparisons among species of *Caenorhabditis* have demonstrated a suite of reproduction-related features that distinguish the highly selfing *C. elegans* (and *C. briggsae*) from its obligately outbreeding relatives, beyond the ability of a 'female' gonad to produce and activate sperm.

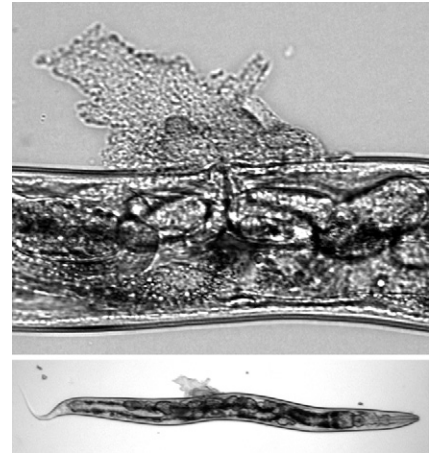


Figure 1. Copulatory plug adhered to the vulva of a female of *Caenorhabditis remanei*. The upper panel shows the copulatory plug of a *C. remanei* female (bottom) that obstructs the vulval opening. Photos by M. Bueno de Mesquita.

Hermaphrodites of *C. elegans* have lost the ability to secrete a potent pheromone to attract males, although *C. elegans* males are still seduced by hetero-specific females that secrete pheromone [13]. Hermaphrodites do not readily search for mates [14] and do not facilitate mating by becoming motionless upon contact with males [15], unlike female relatives. Furthermore, hermaphrodites are less-inclined to mate if their reproductive tract already contains their own sperm, particularly when they are young [16], and frequently eject from their bodies the sperm transferred by males [2,16]. Hermaphrodite sperm also are smaller than male-derived sperm [17], indicating minimal investment in this gamete type by hermaphrodites.

Degradation of mating traits, however, is not limited to hermaphrodites. Male *C. elegans* have smaller sperm [17] and are less-vigorous at mating [13,15] than males of related, obligately outcrossing species. Males of some *C. elegans* wild isolates are sterile, due to deleterious mutation of the *mab-23* gene [4,18]. And, of course, males of some wild isolates lack the ability to place a copulatory plug over the vulva of their mating partner [4], a feat that males of all other *Caenorhabditis* species are able to do (Figure 1). Given the abundance of the non-plugging genotype in nature (31% [3]), it is probably just a matter of time before *C. elegans* males entirely lose the

ability to deposit a copulatory plug. Only a few male *C. elegans* have been collected from nature, out of thousands of sampled animals [9], and population data point to genetically effective outbreeding being exceptionally rare in the wild [9,10]. Consequently, mating of multiple males to the same hermaphrodite in nature should be negligible, obviating the male-benefit of mate-guarding by plugging. All of these characteristics are consistent with the classic expectations of a selfing syndrome — the degeneration of traits associated with outcrossing.

Despite the abundance of evidence for the attrition of traits that enhance the ability to outcross and of sexually selected traits, such as plugging, it is less clear whether this is purely due to relaxed selection for their maintenance, or whether there is active selection against their persistence. If we knew how long *C. elegans* has been reproducing primarily via self-fertilization, then we could assess whether decay due to drift is a sufficient process to explain *C. elegans*' selfing syndrome; however, confidence limits on this age are currently too broad to reach any definitive conclusion [19]. Further insight might come from quantitative genetic approaches that compare phenotypic variation in selfing-syndrome traits to their mutational variance (from mutation-accumulation experiments), or to phenotypic variation of traits not associated with reproductive evolution (e.g., body length). In addition to the phenotypic degeneration noted above, a selfing syndrome should also manifest itself in the *C. elegans* genome [19]. Further comparative

genome analysis within the genus and identification of new, more closely related species will help distinguish drift and selection as evolutionary causes of phenotypic and genomic degradation in selfing lineages of *Caenorhabditis*. In any case, when thinking about evolution in *C. elegans* — and evolution of reproduction-related traits in particular — we must be careful to consider that they likely originated in male–female ancestors [20] under a regime of sexual selection, but that they currently may experience a drastically different selective environment, possibly even a complete absence of selection for the maintenance of traits like copulatory plugging.

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Insect Navigation: Visual Panoramas and the Sky Compass

A new behavioural study shows that honeybees remember visual panoramas in a compass-based coordinate frame, linking together stored visual features of the panorama and signals from their sun-based compass.

Thomas S. Collett

Honeybees navigate over familiar terrain with the help of rich spatial memories. To understand the details of

these memories can be a long drawn out and hard-won process. This particular success story begins one afternoon about fifty years ago, when Lindauer [1] set out a square table

some metres east of a bee hive. He oriented the table so that its corners pointed in the cardinal compass directions and placed a feeding dish on its southern corner. Foraging honeybees soon learnt to visit the southern corner to find this reward. The next morning both hive and table were taken to a new open area so that the surrounding panorama was different. The table was placed in a new direction relative to the hive, but oriented as before, and an empty feeding dish was placed at each corner of the tabletop.