

If decreasing atmospheric CO₂ stabilized the glacial state in the Oligocene, might increasing atmospheric CO₂ from fossil-fuel burning destabilize it in the future? The lesson to be learned here is that we should watch for subtle signs that we are moving from the icehouse world in which Earth has remained for 34 million years into a new, greenhouse world. ■

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BEHAVIOURAL GENETICS

Sex in fruitflies is fruitless

Charalambos P. Kyriacou

The courtship rituals of fruitflies are disrupted by mutations in the *fruitless* gene. A close look at the gene's products — some of which are sex-specific — hints at the neural basis of the flies' behaviour.

Richard Feynman is reported to have said, “Science is a lot like sex. Sometimes something useful comes of it, but that’s not the reason we’re doing it.” In three papers, two published in *Cell*^{1,2}, and one in this issue³ (page 395), science and sex have come together to provide us with something useful — an extraordinary glimpse into how the male and female nervous systems function to generate sexual behaviour in fruitflies (*Drosophila*).

Unlike many British males on a Friday night, *Drosophila* males do not simply jump on the first female they see. Courtship behaviour in *D. melanogaster* is a stereotyped and instinctive sequence of behaviours performed by the male, involving visual, olfactory, gustatory, tactile, acoustic and mechanosensory stimuli being exchanged between the sexes (Fig. 1). The female’s role is considerably less dramatic than the male’s: she simply runs away, gives the odd kick, then mates (or not)⁴.

Normal mature males seldom court other males, but male *fruitless* mutants are bisexual, courting not only females but also other males⁵. In exclusive male company, these

mutants can form bizarre courtship chains, where several males, each chasing and courting the one in front, generate frenzied revolving circles.

The gene mutated in the *fruitless* flies (termed *fru*) was molecularly cloned in 1996, and the putative protein that it encodes was identified as a transcription factor^{6,7}, a regulatory molecule that controls gene expression. A large number of different messenger RNAs can be generated from the *fru* gene, some of which are sex-specific. In particular, an mRNA produced only in males is translated into a protein called Fru^M (for male-specific Fruitless)^{6,7}. This sex-specific production of the *fru* mRNAs is determined by the canonical sex-determination system, the most relevant component of which is the *transformer* gene (or *tra*).

Briefly, the encoded Tra protein binds to very short sequences (13 nucleotides) on the immature *fru* mRNA, to sex-specifically regulate which portions will be ‘spliced’ into the final transcript^{6,7}. (Indeed, Ryner *et al.*⁶ cloned *fru* by looking for genes that contained

Tra-binding sequences.) Similarly, Tra protein binds to the *doublesex* (*dsx*) gene and splices it in male- and female-specific modes (Dsx^M and Dsx^F, respectively)⁸. The Dsx^M and Dsx^F transcription factors mainly determine sexual morphologies⁸, but the sexual identity of the nervous system is shaped by *fru*.

By forcing males to express the female-specific *fruF* transcript, Demir and Dickson¹ produced males that showed the characteristics of the worst-affected *fru* mutants. These males were sterile, they barely courted females and they were more interested in courting males, forming courtship chains. By contrast, females jammed into *fruM* mode mated poorly, produced very few eggs, but — astonishingly — courted other females (Fig. 2), even to the point of forming chains. And an identity crisis of similar epic proportions was observed in females that were ‘masculinized’ using a different *fru*-related genetic trick³. Finally, by feminizing specific abdominal glands in males to produce female pheromones, and placing the altered males with *fruM* females, the sex roles were reversed, so that the females courted the males¹.

In another nifty piece of genetic engineering, both teams^{2,3} generated flies in which they could, among other things, mark the parts of the nervous system (just 2%) that show sex-specific expression of Fru. Further genetic manipulations showed that high levels of male–male courtship result when the communication between these neurons is shut down, or when *fruM* expression in these neurons in males is inhibited^{2,3}. Both studies found that the central nervous system of males and females looked very similar in terms of sex-specific *fru* expression, with few differences between the sexes in the numbers, positions or wiring of cells expressing Fru.

The *fru* products were found in almost all sensory organs that have been implicated in courtship^{2,3}. Olfactory sensory neurons showed some evidence for sexual dimorphisms. Those receptors that respond to pheromones project to certain other brain regions that are larger in males than females, reflecting the fact that sex pheromones have a greater functional significance in male *Drosophila*². By reversibly shutting down the *fru*-expressing olfactory receptors, both in males and in masculinized females in the



Figure 1 | The courtship sequence of *D. melanogaster* males. From left to right, the male orients towards the female, extends a wing and vibrates it, serenading the female with a species-specific love-song. He then licks the female’s genitalia, attempts to copulate, and (maybe) copulates. (Drawings by B. Burnet.)

sex-reversal paradigm outlined above, courtship behaviour declined significantly, implying that these receptors are central to sexual interactions². However, by decreasing *Fru^M* in males just in these neurons, homosexual courtship increased, so normally these olfactory receptors must inhibit male–male interactions³.

So, a single *fru*-encoded genetic switch seems to be sufficient to shift the functioning of the nervous system from male to female mode, irrespective of the morphological sex of the animal. The general absence of large-scale sexual dimorphisms in *fru*-expressing neurons implies that it is the molecules regulated by *fru* that make the difference. Future work will undoubtedly be aimed at finding these molecules, as well as identifying the subset of key neurons that are sufficient to generate male courtship elements. Indeed, Villela *et al.*⁹ have identified neurons downstream of ones expressing *fru* that are implicated in the control of the male's courtship song. Finally, an intriguing and mostly forgotten paper was published 30 years ago¹⁰ about 'lesbian' *Drosophila* females that courted



Figure 2 | Courtship remodelled. A *fru^M* female extends a wing as if 'singing' towards a normal female (reproduced with permission from ref. 1).

other females — apparently because of a genetic factor(s) on chromosome 2 (*fru* is on chromosome 3). Might this long-lost strain have carried a mutation in one of the *fru* target genes?

The work discussed here may well find itself

the focus of attention for those interested in the debate (scientific and political) on the genetic versus environmental bases of human sexuality. Perhaps we should remind ourselves that normal fly sexual preferences, unlike human sexual behaviour, cannot be modulated to any significant extent by altering experience¹¹. ■

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ASTEROIDS

Shaken on impact

Erik Asphaug

A single recent impact may have modified the craters on the asteroid Eros into the pattern we see today. This finding has implications for how we view the structure of asteroids — and for addressing any hazards they present.

Asteroids seem to get stranger with every passing year. Thomas and Robinson's finding (page 366 of this issue)¹ — that impact-induced vibrations of an asteroid may be the dominant mechanism reshaping its surface — shakes things up still further. In the case of the well-studied asteroid Eros, the authors link this resurfacing mechanism to the recent impact of a meteoroid that left a particularly large crater. They thereby make the first detailed mechanical connection between surface observations and an asteroid's global geology. The authors conclude that Eros, a rocky asteroid 33 by 13 by 13 kilometres in size, has a relatively homogeneous interior that transmits seismic shocks efficiently and is mantled by a hundred metres or more of regolith. (Regolith is the loose soil-like material familiar from pictures of the surface of the Moon.) This might not come as a surprise, given Eros's appearance², but for the first time, the authors provide convincing evidence that makes this conclusion more than just reasonable conjecture.

Thomas and Robinson's discovery marks another stage in the journey asteroids have taken from insignificance, through notoriety, into the mainstream of scientific interest. The turning point came in the 1980s, when an asteroid was found to be responsible for the

greatest calamity to befall Earth's biosphere since the Permian era — an impact 65 million years ago in present-day Mexico that is postulated, among other things, to have wiped out the dinosaurs. That got people's attention. But the geological subtleties of asteroids remained largely unappreciated for a further ten years. This situation began to change with the first detailed ground-based radar observations³, and the Galileo mission's fly-by of the asteroids Ida and Gaspra⁴. Now, a new generation of scientists is appreciating asteroids as geological entities^{2,5,6}.

If Thomas and Robinson's hypothesis of seismic shaking¹ is correct, then the cratering history of any asteroid is complex. Impacts of small meteoroids make the surface heavily cratered, giving it an 'old' look, whereas impacts of larger meteoroids — by causing the surface to vibrate — erase smaller craters, making the asteroid appear 'young'. This asteroidal Botox calls into question the habit of dating asteroid surfaces through their cratering record: although the passage of time is indeed recorded here, so too is internal structure. A young asteroid of the type that resembles a rubble pile, for instance, is more capable of damping vibrations, and might retain more craters — and so appear older — than an

ancient, 'competent' asteroid that has a more monolithic interior and thus transmits seismic energy more effectively. But Thomas and Robinson's work also opens up a new way of looking at asteroids generally. It shows how we might gauge interior structure from surface observations: craters and other landforms, and their degradation, could be used as proxies for seismic data.

The idea of seismic processes resurfacing asteroids is not itself new. The formation of the large crater Stickney on Phobos (Fig. 1, overleaf), a martian moon about the size of Eros and perhaps a captured asteroid, was modelled⁷ 12 years ago using a computational tool called a hydrocode to simulate the effect of the high-velocity impact. The simulation showed that seismic resurfacing could erase craters smaller than about 100 metres in diameter, and significantly degrade larger craters. The same method was later used to show⁸ that the jolting of the asteroid Gaspra by large impacts could lead to the unusual distribution of its crater sizes. In an argument analogous to that used by Thomas and Robinson for Eros, the asteroid Ida was suggested⁹ to have a relatively monolithic deep interior, given evidence that stress energy was transmitted from a large impact structure at one end to