

Battle of the sexes

SIR — Sexual conflict can result in rapid evolutionary change. Rice¹ found that male and female fruitflies, *Drosophila melanogaster*, are continually forced to counteract adaptations in the other sex to maintain their fitness (see also the discussion of this paper in News and Views²). Rice concluded that “intersexual coevolution... [can] contribute substantially to genetic divergence among physically isolated or semi-isolated populations”. But does sexual conflict invariably operate as an ‘engine of speciation’? There is at least one case where it appears to have the opposite effect.

The guppy, *Poecilia reticulata*, is a small poeciliid fish, native to Trinidad and northeast South America. It is an ovoviviparous species with a promiscuous mating system. Guppy populations in Trinidad show marked differentiation and have become a classic example of evolution in action³. Natural selection, in the guise of predators, accounts for much of the variation; experiments have revealed rapid population divergence following a shift in predation regime. For example, heritable changes in male colour patterns⁴, life-history traits⁵ and antipredator behaviour⁶ occur within a few years (from 10 to 100 generations) of a reduction in predator pressure.

It is not only natural selection that drives evolution in this species; sexual selection is also a significant diversifying agent with the potential to reinforce population differences that predators have generated. Female guppies exert choice and base their mating preferences on individually variable male colour patterns. Female preferences and male coloration co-vary across populations⁷. Houde⁸ has uncovered a genetic correlation between

male coloration and female choice which may facilitate speciation⁹. Once mating has occurred, females can store sperm and fertilize several broods without further contact with a male. A single female can even found a viable population¹⁰. The genetic drift resulting from such severe founder events may further magnify population differences.

Although many of the elements required for rapid evolution are present, guppy populations, in Trinidad at least, do not appear to be speciating³. Populations that have been separate for about 2 million generations^{11,12} will interbreed if given the opportunity to do so^{13,14}. How might this paradox be resolved?

It seems that while many aspects of the behaviour and biology of female guppies hasten differentiation, a number of male traits hinder it. Wild female guppies are subject to a barrage of sneaky mating attempts, receiving, on average, one per minute¹⁵. The relative success rate of sneaky matings is unknown. However, the

high incidence of sneaky matings is such that only a few need to be successful to undermine female choice. Female preference may be further compromised by competitive mating among males^{13,16}. In addition, male guppies are much more likely to emigrate than females (D. N. Reznick, personal communication). The net result is that the geographical scale of gene flow is large relative to the scale of the selection regime³ and reproductive isolation, which is the precursor of speciation, has little opportunity to develop. Of course, sexual conflict is not the only factor that shapes the destiny of guppy populations, but it must play a significant, if previously unrecognized, role. The battle of the sexes does indeed have profound evolutionary consequences.

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Na⁺ channel subunits and Ig domains

SIR — Voltage-gated sodium channels isolated from brain cells are heterotrimeric complexes composed of a central, pore-forming α -subunit, of relative molecular mass 260,000 (M_r 260K), and two auxiliary subunits, β_1 (36K) and β_2 (33K) (ref. 1). The α -subunit is a polytopic transmembrane glycoprotein, whereas the β_1 and β_2 subunits are single membrane-spanning glycoproteins. The β_1 and β_2 subunits are unique among ion-channel subunits studied to date in that their extracellular domains contain immunoglobulin-like motifs, similar to those found in many cell-adhesion molecules². In addition, the β_2 subunit has a segment with striking amino-acid sequence similarity to the cell-adhesion molecule contactin². Because nearly all of the immunoglobulin-like motifs so far discovered interact with extracellular protein ligands³, the β_1 and β_2 sodium-channel subunits probably also serve this function. As sodium channels are highly localized in neurons and are immobilized in the neuronal plasma membrane⁴, interaction of the β_1 and β_2 subunits with extracellular proteins could function in the targeting, membrane insertion and immobilization of sodium channels.

Previous analyses of the structures of immunoglobulin-like motifs have defined

three structural sets: the C1-, C2- and V-sets³. According to these previous criteria, most cell-adhesion molecules in the nervous system, including contactin, NCAM and myelin-associated glycoprotein, are included in the C2-set of immunoglobulin-like motifs³. But based on analysis of the many more immunoglobulin-like motifs that have become available since the initial classification, a revised structural classification and revised consensus sequences for the C2-set and the V-set were proposed in a recent review⁵. In this new structural classification, the neural cell-adhesion molecules contactin, NCAM, myelin-associated glycoprotein, DCC, DM-GRASP, telencephalin and Thy-1 are all in the V-set rather than the C2-set.

The consensus sequence derived from analysis of the sequences of these neural cell-adhesion molecules and other V-set immunoglobulin-like motifs is illustrated in the figure, together with the corresponding residues from the β_1 and β_2 subunits. This comparison shows that the immunoglobulin-like motifs of the β_1 and β_2 subunits belong to the V-set according to this new consensus sequence. Of eight positions in the consensus having predicted hydrophobic amino acids, β_1 contains seven and β_2 six. Both subunits contain a conserved tyrosine in the appropriate

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V-like	Gxx*x*xxC ... *xW ... +* ... Lx*xx*xxxDx#xYxC ... **x**
β_2	LPCTFN <u>SC</u> ... <u>LNW</u> ... <u>KI</u> ... <u>VT</u> LKNVQLEDEGI <u>YNC</u> ... <u>IY</u> LOV
β_1	FK <u>IL</u> C <u>ISC</u> ... TEW ... <u>KI</u> ... <u>IF</u> I <u>T</u> NV <u>T</u> Y <u>N</u> HSGDY <u>EC</u> ... <u>I</u> H <u>LE</u> V

Consensus alignment of immunoglobulin V-like domains. Asterisks, hydrophobic amino acids; crosses, basic amino acids; hashes, Gly, Ala, Asp; X, any amino acid.