



Figure 2. Circuit diagram detailing the connectivity of the L2-pathway, as described in [1].

In each cartridge of the lamina, the axon terminals of photoreceptors R1–6 converge onto two lamina neurons, L1 and L2. There, L2 also contacts an L4-cell, which in turn contacts L2- and L4-cells in the posterior cartridges in a bidirectional way. Within the corresponding column of the medulla, the L2-cell synapses in parallel onto Tm1 and Tm2. Tm2 receives additional input from the L4-cell originating in the home cartridge as well as from L4-cells located in the anterior cartridges, both in a unidirectional way.

network represented by L2–L4–Tm2 connectivity in the lamina, as well as in the medulla, might represent a spatial filter for the signal in the L2-pathway, possibly adapting the system to different light conditions by pooling the signals from neighboring cartridges before feeding into the motion detector. Alternatively, this network’s sole action might be to transform the coordinate system from a hexagonal array onto an orthogonal one, bringing the three axes of symmetry of the facet raster onto a system with two main axes only. However, neither of the above functions would require any directionality, as is present in the network.

In contrast, directionality is required for the most exciting hypothesis offered by the authors: the possibility that, in Tm2, the direct input from L2 is compared with the delayed input from the anterior location provided by L4. This would postulate that Tm2 is indeed the first site where direction selectivity originates with a particular sensitivity for front-to-back motion, corresponding to the output of the multiplier in one subunit of the Reichardt detector (Figure 1C). Testing

these different hypotheses will require direct recordings from Tm2 cells, either optical or electrical, and/or silencing them, again in combination with a behavioral or electrical read-out. Whatever the answer, the paper by Takemura *et al.* [1] brings us closer to the heart of the fly motion detection circuitry that has been hidden in the jungle of the fly optic lobe for so long.

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## Social Evolution: Evolving Sex Ratios

A recent study comparing sex ratios produced by experimental evolution in spider mites with those predicted by Hamilton’s Local Mate Competition Theory clearly demonstrates Evolutionary Theory’s success as a quantitatively predictive science.

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A recent paper [1] has provided powerful experimental evidence that

William Hamilton’s Local Mate Competition (LMC) Theory, and by extension Evolutionary Theory, is in fact a successfully predictive science. The authors subjected spider mites

to different population structures, differing in the number of mated females contributing to local mating populations. LMC Theory predicts that these population structures will select for mothers to produce offspring in different, specific sex ratios. The mite populations evolved sex ratio responses that were both qualitatively and quantitatively in agreement with LMC predictions. By applying a methodology (experimental evolution) that has not been previously used in this area of evolutionary biology, the authors add a decisive missing piece that corroborates decades of previous theoretical and empirical work on adaptive sex ratios.

In one of the first recorded references to sex ratios in animals, God is alleged to have instructed Noah to collect one male and one female of each species and put them on his Ark in order to repopulate the Earth after the Great Flood (Genesis 6: 7–20, in the King James version of the Bible). The clear implication was that a one to one sex ratio (0.5 males) was the norm at the beginning. Fast forward a few millennia. While recognizing that, in the preponderance of familiar animals (mammals, birds, and so on), one to one sex ratios were the norm, Charles Darwin also recognized that, in many organisms less familiar to the writers of Genesis, sex ratios often varied greatly from the standard one to one. After struggling with the question, he wrote [2]: “I formally thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future.”

Warm on Darwin’s heels, Ronald Fisher [3] proposed an elegant explanation for the widely observed one to one. He recognized that, in sexually reproducing organisms, half of the genetic contribution to each future generation came from females and half came from males. He reasoned that, this being the case, if either sex were in a minority, then individuals of that sex would on average represent a more valuable vehicle for propagating genes. It followed that mothers producing an excess of the rare sex would be at an advantage and that this advantage would spread until the rare sex was no

longer rare [3]. This provided a satisfactory ultimate explanation of the familiar one to one sex ratio observed in most vertebrates and many other organisms. Subsequent authors have correctly emphasized the crucial role of sex-determining mechanisms [4] in providing the proximal mechanism that often (but not always) constrains the potential for selection for different sex ratios to act [5].

However, many animals often produce offspring in broods that exhibit strong to extreme female biased sex ratios. William Hamilton [6] recognized that these female-biased species also often exhibit highly structured populations — populations in which one or a few mated females contribute brood to localised mating populations from which the mated daughters disperse. Further, Hamilton recognized that Fisher’s explanation for one to one sex ratios depended critically on the unstated assumption that individuals exhibit open (panmictic) population structures, meaning essentially that all males have roughly equal access to all females, and *vice versa*. Having already proposed the concept of inclusive fitness, grasped its importance in identifying the proper target of selection, and then developing its theoretic framework, Hamilton extended those ideas and presented an explicit argument that he termed ‘Local Mate Competition’ (LMC) to explain female bias under conditions of high population structure ([6,7]; see [8] for a description of historical context). His contribution incorporated and greatly extended Ronald Fisher’s general explanation of 50:50 sex ratios.

A key and very powerful aspect of Hamilton’s theory was that it makes precise quantitative predictions of the sex ratio expected under specific intensities of LMC. Importantly, several types of predictions emerge. One prediction refers to a *population mean response*: populations that experience more extreme LMC should exhibit more female-biased sex ratios. A second prediction refers to *individual responses and ability to adjust sex ratios*: a female should be able to adjust her sex ratio according to the local LMC conditions, and do so in very specific ways. A third prediction concerns the *variance of sex ratios*: females should produce LMC sex ratios that exhibit

lower than binomial variance [9]. Subsequent tests have been overwhelmingly supportive of the basic idea and its extensions. To date, support for specific aspects of LMC theory, and for Fisher–Hamilton sex allocation more generally, has come from a variety of empirical approaches. These include correlational studies, extensive experimental manipulations of one or more parameters in LMC models, and comparative analyses, in organisms ranging from wasps to malaria parasites to flatworms [5,10–13]. This broad fit between theory and its tests has become a cornerstone pointing to both the qualitative and the quantitative predictive power of evolutionary theory in explaining adaptations. Hamilton commented that sex allocation theory in general and LMC in particular is “the section of evolutionary theory that best proves the power and accuracy of the Neodarwinian paradigm as a whole” [8].

Until now, however, we have lacked direct evidence that the conditions Hamilton identified actually *select* for LMC sex ratio behaviour *de novo* [14]. This is where Macke *et al.* [1] break important new ground by providing the first experiment in which an organism that is both able to adjust its sex ratio and shows the ability to respond to selection on sex ratio [1] actually responds to different LMC intensities in ways that are in quantitative accordance with the theory. Their decisive test shows that the different average LMC conditions actually do *select* for different average sex ratios as theory predicts, that organisms can *respond to that selection*, and that they do so in quantitative agreement with theoretic predictions. They further show that the ability for individual females to adjust their sex ratios is also influenced by the selective regime [1,11]. Under intense, invariant LMC conditions, the ability to adjust sex ratios is lost. These evolutionary responses to different experimental conditions mirror the results from a multitude of behavioural studies at the phenotypic level [5,10–13], and strengthen the interpretation that such sex-ratio behaviour is in fact a product of selection imposed by the LMC processes that Hamilton envisioned. This study therefore directly and successfully addresses previous *legitimate* concerns that the theory had

not been tested via an explicit selection experiment [14]. Moreover, as well as completely knocking away the support from under any argument that evolution is not a quantitatively predictive science, this study very nicely ties up a loose end for what has been one of the most successful branches of evolutionary biology.

Further quantitative tests of specific LMC predictions employing the experimental selection approach used by Macke *et al.* [1] over a wider range of population structures are certainly needed, as are additional tests of adaptive sex ratio evolution in other organisms. However, critics of the predictive power of Evolutionary Theory writ large, and William Hamilton's fundamental insight of Inclusive Fitness as extended to Local

Mate Competition Theory in particular, now can turn their attention elsewhere.

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## Reputation Management: In Autism, Generosity Is Its Own Reward

A recent study has found that autistic people donate the same to charity regardless of whether they are observed. This is not because they are oblivious to others, but because they are free of hypocrisy.

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In a recent paper Izuma *et al.* [1] have confirmed that as far as ordinary people are concerned, it is not enough to give to charity, you have to be seen to be charitable, but this does not apply to autism. Ordinary people behave more altruistically if they are observed [2]. They care passionately about their reputation and this in turn hugely benefits cooperation [3,4]. This idea may seem to be contradicted by recent reports in the UK press of excessively high salary increases awarded to CEOs of big companies. This was greeted with outrage, but no CEO offered to forgo their increase. In the eyes of the public they suffered a loss of reputation, but it seemed they didn't care.

According to the new study [1], there is in fact a group of people who genuinely do not care about their reputation in the eyes of others: individuals with autism. An elegant experiment showed that they were insensitive to reputation. Izuma *et al.*

[1] suggest that this is a consequence of mindblindness, or lack of 'Theory of Mind'. Autism has become a model for studying Theory of Mind or mentalizing, that is, the ability to attribute intentions and beliefs to others to predict their behaviour. This ability is independent of the ability to attribute cause and effect to physical events, an ability that is intact in autism [5].

Mindblindness attempts to explain social impairments in autism that involve mentalizing. It is silent on social impairments that may often be present in autism, but do not involve mentalizing, for instance a lack of social interest. A refinement in the understanding of social impairments in autism will have benefits for understanding more precisely which social skills are at their disposal. The study by Izuma *et al.* [1] contributes to this enterprise in several important ways. It addresses two hitherto outstanding questions [6]. First, is mentalizing a critical mechanism in reputation management? Second, to

what extent are autistic people subject to the audience effect, that is, to what extent do they change their behaviour in the presence of others?

There has already been speculation on the basis of a neuroimaging study of a trust game [7] that individuals with autism do not care about their reputation [8]. Thanks to the ingenious design by Izuma *et al.* [1] we now know this to be true. They compared performance in the presence and absence of an observer in two situations, one where image scoring was an issue and another where it was not. For the former they used a version of the Dictator game. The participant was given an initial endowment and then, on each trial, could decide whether or not to donate a variable proportion of their endowment to a charity. In one condition an observer was present, in another absent.

As expected from previous studies, ordinary people were more generous in making charitable donations when an observer was present. They care about their reputation in the eyes of the observer and hence they donate more than they would donate anonymously. We can call this hypocrisy. People display high mindedness only if this serves to enhance their image, but otherwise they behave quite selfishly. One might predict that even those CEOs who were recently castigated