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documented when viewing video sequences of social interactions in an unconstrained manner [5]. Alternatively, however, such difficulties in autism might reflect more fundamental problems in *perceiving* social stimuli, including faces and voices [6]; even under more constrained viewing conditions, individuals with autism seem to show poorer identity and emotion recognition [7].

Pellicano *et al.*'s [4] study provides clear evidence of poor social perception, revealing that adaptation of face mechanisms is severely abnormal in autism. The children with autism in their study were clearly attending to the faces as their performance in baseline conditions was similar to that of the typical children, yet fundamental differences in face-processing were evident. It is not simply the case, therefore, that children with autism were uninterested in the stimuli that Pellicano *et al.* used. Rather, it seems that their face-recognition mechanisms were not adapting to the new stimuli. The function of adaptation, in other domains of visual processing, seems to be to provide stability of visual categorisation, by 're-tuning' perceptual mechanisms to take account of prevailing conditions (for example, ensuring that a grey object will look grey even when

appearing under coloured illuminants). If this does not operate for face perception in autism, categorisation of faces may be unstable from one day to the next, even though the individual can in each case distinguish one stimulus from another.

Two final points also merit particular discussion. First, an important question for future research to address is whether face adaptation deficits have substantial consequences for social and communicative processing in general. Suggestive evidence that they do is already apparent from Pellicano *et al.*'s [4] finding that the severity of autistic symptoms in each of their individuals with autism showed a clear relationship to their deficit in adaptation. Second, the work also demonstrates neatly the value of studying the interplay between functional neural subcomponents in disorders, rather than between brain regions. fMRI studies suggest that when attention to faces is maintained, children with autism recruit the same neural areas when viewing faces that typical children do, suggesting 'normal' face processing. Instead, the trick to understanding face processing abnormalities in autism may not simply lie in gross activation or anatomical differences, but rather

in the substantial, if subtle, interactions between representations sharing the same neural underpinnings.

References

1. Tsao, D.Y., and Freiwald, W.A. (2006). What's so special about the average face? *Trends Cogn. Sci.* 10, 391–393.
2. Leopold, D.A., O'Toole, A.J., Vetter, T., and Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nat. Neurosci.* 4, 89–94.
3. Rhodes, G., and Jeffery, L. (2006). Adaptive norm-based coding of facial identity. *Vision Res.* 46, 2977–2987.
4. Pellicano, E., Jeffery, L., and Burr, D. (2007). Abnormal adaptive face-coding mechanisms in children with autism. *Curr. Biol.* 17, 1508–1512.
5. Klin, A., Jones, W., Schultz, R., and Volkmar, F. (2003). The enactive mind, or from actions to cognition: lessons from autism. *Phil. Trans. R. Soc. Lond. (B)* 358, 345–360.
6. Plaisted, K., Saksida, L., Alcantara, J., and Weisblatt, E. (2003). Towards an understanding of the mechanisms of weak central coherence effects: experiments in visual and configural learning and auditory perception. *Phil. Trans. R. Soc. Lond. (B)* 358, 375–386.
7. Behrmann, M., Thomas, C., and Humphreys, K. (2006). Seeing it differently: visual processing in autism. *Trends Cogn. Sci.* 10, 258–264.

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DOI: 10.1016/j.cub.2007.08.003

Sexual Selection: Signals to Die for

Sexual signals are conspicuous and are typically assumed to be energetically costly, which keeps them honest. A recent study on fireflies has found that signal production is energetically cheap, but signalling remains expensive because of eavesdropping predators.

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The sexual signals that males use to serenade potential mates are typically extravagant and conspicuous [1]. These signal characteristics are great because they enhance reproductive success, for example by making signallers easy to find. But they also make signals costly if they

deplete the energy reserves needed for reproduction, or if they alert predators to the presence of a snack in the form of the signaller. Signal costs such as these are important because they ensure signals are honest indicators of mate quality [1,2]. That is, only high quality males are able to produce the costly signals females pay attention to, much as Rolls Royce motorcars and private jets are

honest signals of human wealth. These costs also act as a brake on signal exaggeration, and energetic and predation costs have been widely documented. However, multiple signal costs are rarely investigated in one species so we only have a rudimentary understanding of the relative importance of different costs in signal evolution. A new study by Woods *et al.* [3] has partly redressed this gap in our understanding by quantifying the energetic and predation costs of bioluminescent signals in *Photinus* fireflies. Their results contrast somewhat with findings in other groups, but it is not entirely clear why.

One of the few instances where the multiple costs of a sexual signal

has been investigated is the classic work on the tungara frog and the predator that exploits its sexual signal, the fringe-lipped bat [4–6]. Male frogs produce conspicuous, energetically expensive calls to attract female frogs, but unfortunately for them, the same call characteristics preferred by females are also preferred by the frog-eating bats. This puts male frogs in an evolutionary bind. They have to call a specific way to attract females and reproduce, but by doing so, they greatly increase the chance that they will become bat food, with obvious negative fitness consequences. This means that over evolutionary time, tungara frog calls and calling behaviour have been moulded by these conflicting selection pressures [4–6]. The fireflies studied by Woods and co-workers also utilize a conspicuous courtship signal. In the firefly system, the sexual signals are the flashes produced by the firefly lantern, and although the results of this work in some ways reflect the bat–frog findings, there are some important differences too.

Male *Photinus* fireflies attract mates by flying around in the dark emitting flashes of bioluminescent light, with species-specific flash rates and durations. When a receptive female sees the flash, she responds by signalling back with a flash of her own. This attracts the male, who then flies toward her, lands and undertakes a lengthy courtship dialogue of bioluminescent flashes with the female [7,8]. Females prefer the most conspicuous males: those capable of signalling with long flash durations and/or high flash rates [9–11]. As in the frog study, however, signalling is mortally risky for fireflies because predatory *Photuris* fireflies exploit the courtship duetting of *Photinus* fireflies [12–14]. They do this by imitating the flashes of receptive *Photinus* females, and attracting unsuspecting males which they then eat [15]. Love is never easy. This deception was noted sometime ago [15], but the energetic costs of signalling and, surprisingly, the predation costs associated with signalling had not been investigated.

Woods *et al.* [3] have addressed both issues. They used respirometry to estimate the energy costs of signalling — using CO₂ production as a measure of metabolic rate — of individual fireflies when they were flashing and when they were resting. Cleverly, they also investigated the possibility that maintaining a bioluminescent capability may in itself be costly, by comparing the resting metabolic rates of bioluminescent fireflies and non-bioluminescent lampyrid species. The results of this aspect of the study are fascinating, not only because the energy requirements of bioluminescence have never been measured previously, but also because it appears that flashing is highly energy efficient. In fact, it is more energetically costly for a firefly to walk than to flash. Additionally, there was no difference in resting metabolic rate of bioluminescent and non-bioluminescent species — this is not a perfect comparison by any stretch of the imagination, but it makes the salient point nonetheless. So although higher flash rates consume more energy than low flash rates, the energetic expenditure required for the conspicuous courtship signal of these fireflies is relatively minor in the grand scheme of things. This is surprising because sexual selection theory predicts sexual signals should be costly to honestly reflect mate quality and the cost frequently assumed to impose honesty is energy expenditure [1]. This assumption is supported by the energetic costs of many courtship signals. For example, the calls male crickets use to attract females can raise male metabolic rates by ten-fold or more [16,17]. It is not clear why there is this massive difference in the costs of signalling, but it may have to do with the fact that female fireflies also signal, although duetting also occurs in crickets and their calls are costly. In any case the firefly study suggests measuring the energetic demands of sexual signals in other species is not without merit.

The predation costs of firefly signals were investigated in a separate field-based experiment

by measuring predator attraction to simulated firefly courtship signals and non-signalling controls. These results showed that predatory fireflies apparently impose major costs on the courtship signals. Traps containing flashing signals were significantly more attractive to predatory fireflies than those containing non-flashing controls. Furthermore, the experiments revealed that the higher flashing rates preferred by the (non-predatory) females that males are trying to attract are also more conspicuous to predators and increase the likelihood of male death. Consequently, and as with the frog calls, firefly courtship signals are likely to represent an evolutionary compromise between attracting and obtaining mates, and minimising predation. This assertion is consistent with other data like shifts in signal colour and receptor sensitivity, as well as changes in signalling behaviour [12]. Relative to the energetic investment required for courtship, predation costs seem to be of tremendous importance in the evolution of bioluminescent signals in fireflies.

The conclusion that natural selection through predation is so prominent in shaping the evolution of conspicuous courtship signals in fireflies augments the findings of a recent study of field crickets [18]. Male crickets produce conspicuous calls that attract females, but again the signal is exploited, this time by an acoustically orienting fly. Zuk and co-workers [18] found that parasitism by the fly seems to have favoured the spread of a ‘flatwing’ cricket morph that is unable to produce a courtship signal. Silent crickets escape parasitism because the fly uses courtship song to locate and parasitize amorous males. In less than twenty generations, the ‘silent’ flatwing morph became the most prevalent type of male in the population, despite the fact that these males are unable to court and attract females in the conventional way. Instead, flatwing males act as ‘satellites’ to the few remaining normal males and intercept females attracted to their songs.

Flatwings have in effect become parasites on singers. Although all this cricket evidence is correlational, it is entirely consistent with predators causing rapid evolutionary change in a conspicuous sexual signal.

Because the presence of predators does not necessarily overlap perfectly with prey distribution, either in space or time, selection on prey sexual signals through predation will also vary. Furthermore, because courtship signals are often essential for species recognition, localised variation in predator-applied selection on sexual signals could lead to population divergence and eventual speciation [19]. This is a distinct possibility for fireflies since *Photuris* predators only overlap with a subset of the *Photinus* populations. In the mean time, and wherever you are, conspicuous signallers beware.

References

1. Maynard Smith, J., and Harper, D.C.G. (2004). *Animal Signals* (New York: Oxford University Press).
2. Grafen, A. (1990). Biological signals as handicaps. *J. Theor. Biol.* 144, 517–546.
3. Woods, W.A., Jr., Hendrickson, H., Mason, J., and Lewis, S.M. (2007). Energy and predation costs of firefly courtship signals. *Am. Nat.*, in press.
4. Tuttle, M.D., and Ryan, M.J. (1981). Bat predation and the evolution of frog vocalizations in the Neotropics. *Science* 214, 677–678.
5. Ryan, M.J., Tuttle, M.D., and Rand, A.S. (1982). Bat predation and sexual advertisement in a Neotropical Anuran. *Am. Nat.* 119, 136–139.
6. Ryan, M.J. (1985). Energetic efficiency of vocalisation by the frog *Physalaemus pustulosus*. *J. Exp. Biol.* 116, 47–52.
7. Venzl, F.V., and Carlson, A.D. (1998). Proximate mechanisms of sexual selection in the firefly *Photinus pyralis* (Coleoptera: Lampyridae). *J. Insect Behav.* 11, 191–207.
8. Demary, K., Michaelidis, C.I., and Lewis, S.M. (2006). Firefly courtship: behavioural and morphological predictors of male mating success in *Photinus greeni*. *Ethology* 112, 485–492.
9. Cratsley, C.K., and Lewis, S.M. (2003). Female preference for male courtship flashes in *Photinus ignites* fireflies. *Behav. Ecol.* 14, 135–140.
10. Branham, M.A., and Greenfield, M.D. (1996). Flashing males win mate success. *Nature* 381, 745–746.
11. Michaelidis, C.I., Demary, K.C., and Lewis, S.M. (2006). Male courtship signals and female courtship assessment in *Photinus greeni* fireflies. *Behav. Ecol.* 17, 329–335.
12. Lloyd, J.E. (1965). Aggressive mimicry in *Photuris*: firefly femme fatales. *Science* 149, 653–654.
13. Nelson, S., Carlson, A.D., and Copeland, J. (1975). Mating-induced behavioural switch in female fireflies. *Nature* 255, 626–627.
14. Lloyd, J.E., and Wing, S.R. (1983). Nocturnal aerial predation of fireflies by light-seeking females. *Science* 222, 634–635.
15. Lloyd, J.E. (1997). Firefly mating ecology, selection and evolution. In *The Evolution of Mating Systems in Insects and Arachnids*, J.C. Choe and B.J. Crespi, eds. (Cambridge: Cambridge University Press), pp. 184–192.
16. Bailey, W.J., Withers, P.C., Endersby, M., and Gaull, K. (1993). The energetic costs of calling in the bushcricket *Requena verticalis* (Orthoptera: Tettigonidae: Listroselidinae). *J. Exp. Biol.* 178, 21–37.
17. Prestwich, K.N. (1994). The energetics of acoustic signalling in anurans and insects. *Amer. Zool.* 34, 625–643.
18. Zuk, M., Rotenberry, J.T., and Tinghitella, R.M. (2006). Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biol. Lett.* 2, 521–524.
19. Zuk, M., and Kolluru, G.R. (1998). Exploitation of sexual signals by predators and parasitoids. *Quart. Rev. Biol.* 73, 415–438.

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DOI: 10.1016/j.cub.2007.08.001