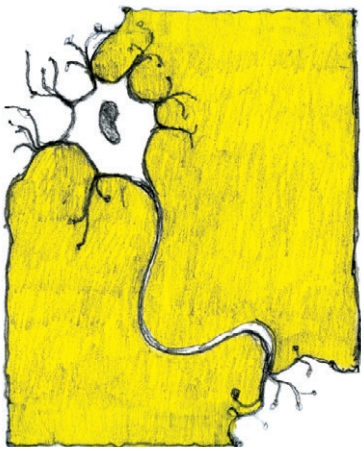
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

SOCIAL CONTEXT



HONEY BEE PEER PRESSURE

The timing of when we sleep, eat and work is somewhat determined by social cues – when others in our house go to bed, what time our friend can meet for breakfast at the café, and if our boss is at the lab yet. It is also affected by how old we are, and honey bees are much the same. Within the hive there exists a fascinating division of labor. At approximately 2–3 weeks of adult life honey bees work tirelessly inside the hive. At this stage they are on-call, responsible for brood care, 'nursing' the younger bees for 24 h a day. Later in adulthood honey bees make a career change. In the final 1–2 weeks of life, bees begin to venture outside the hive to forage for nectar and pollen but they only go out and forage during daylight hours.

The change in overt behavioral patterns, how active animals are throughout the day or night, is also reflected at the cellular level through the cycling of certain genes in clock cells, which are thought to act as pacemakers. Yair Shemesh and colleagues, at The Hebrew University of Jerusalem, recently added to our understanding of how the social environment within the hive sets the daily activity of honey bees with their work published in *The Journal of Neuroscience*.

The team first asked whether direct contact between the nurse bees and the brood is required to regulate the daily rhythm of clock gene expression within clock cells and second, whether the 24 h active care exhibited by the nurse bees is dependent on direct physical contact with the brood. In three parallel experiments they measured gene expression and behavioral patterns of nurse bees in specific social contexts: nurse aged adults caged on broodless honey comb inside the hive, nurse bees caged on a brood-containing comb outside the hive, and nurse bees caged on a broodless comb outside the hive. These experimental parameters differentiate between the seemingly restrictive age dependent developmental patterns – early nursing and later foraging – of honey bee behavior. By separating the nurse aged adults from the brood and forcing them to function as workers, researchers can ask whether age or social influence determine the honey bees' work status, as nurse or forager.

Shemesh and co-workers found that the nursing bees switched to a daily pattern of behavior soon after release from direct contact with the brood hive, rather than their constant 24 h nursing pattern. This behavioral change was also reflected in changes in clock gene expression. Whereas nurse bees had no or very weak cycling of their clock genes while living in the hive with the brood, after being transferred from the hive to small broodless cages the nurse bees developed a forager-like molecular clock expression pattern.

These results demonstrate the remarkable influence that social context plays at multiple levels from molecular biology to behavior; not only is honey bee nursing activity a reflection of social interactions with the brood but this behavior is revealed at a fundamental level through the cycling of specific genes.

10.1242/jeb.049676

Shemesh, Y., Eban-Rothschild, A., Cohen, M. and Bloch, G. (2010). Molecular dynamics and social regulation of context-dependent plasticity in the circadian clockwork of the honey bee. *J. Neurosci.* **30**, 12517-12525.

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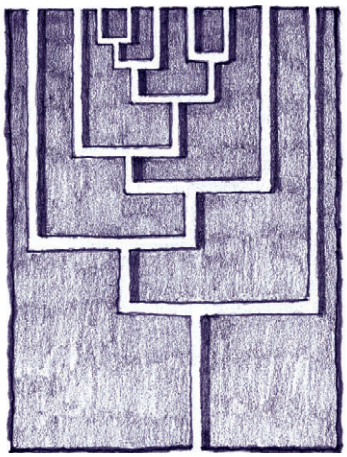
SEX DIFFERENCES



BULLYING MAKES FLIES GET IN FIGHTS

Pheromones are strong chemical cues that are sometimes thought to induce automatic behavioral responses, particularly in so-called 'simple animals' like fruit flies. Male flies fight with each other for the right to feed and mate on food patches, but when a female drops in, a male will court rather than act aggressively toward her. It was thought that a male determines the sex of an intruder to his food patch by sampling the strange fly's pheromones. Based on this, María de la Paz Fernández, Yick-Bun Chan and their colleagues predicted that a female fly expressing male pheromones would be quickly attacked by a resource-guarding male.

The authors tested their hypothesis by genetically engineering female flies to have a partial male pheromonal profile, though notably not including a male chemical called cVA that was recently described as an aggression-promoting pheromone. Fernández and Chan paired these masculinized females with wild-type males in small arenas with a dollop of food. The males displayed aggression toward these male-smelling females, which never happened toward wild-type females. However, males mated quite readily with the transformed females despite their smell. This made the authors curious whether females would be attacked or courted if they smelled feminine but behaved like males.

They engineered females by masculinizing their nervous systems but not their pheromones, paired them with wild-type males, and watched to see if the flies fought. They did, and they fought even more than males with females that smelled male. However, the males rarely initiated these fights. Rather, it was the females with masculinized brains who typically lunged aggressively toward the males, and because the males responded in kind, they rarely mated successfully.

Next, the authors wondered whether the combination of pheromones and behavior was enough to effectively change regular male–female interactions into complete male–male aggression, or *vice versa*. Fernández and Chan combined their earlier experiments by constructing females that had both masculinized nervous systems and the partially masculinized pheromones that they had used before. These females fought with wild-type males just as much as wild-type males did, but again, the fights were more commonly initiated by the females rather than the males, and a low level of successful mating persisted in these match-ups.

Finally, Fernández and Chan repeated the experiments with male flies. Feminizing either a male's nervous system or the pheromones resulted in only very slightly decreased aggression between a wild-type and a transformed male. However, altering both pheromones and behavior reduced aggression dramatically, though some fighting persisted. Wild-type males rarely attempted to mate with males who had feminized behaviors, but the combination of pheromones and behavior greatly enhanced mating attempts, approaching the levels of typical male–female interactions.

These results from Fernández, Chan and colleagues suggest that although most of the differences between normal male–female and male–male encounters can be reversed by endowing females with a particular set of male pheromones and male-like aggressive behavior, some parts of the story are still left out. It is possible that one of the missing pieces is the aggression-promoting chemical cVA, which is produced by a different mechanism from the one transformed in this study. However, one message is clear: flies pay attention to more than just pheromones when determining whether to fight or court a stranger.

10.1242/jeb.049668

Fernández, M. P., Chan, Y.-B., Yew, J. Y., Billeter, J.-C., Dreisewerd, K., Levine, J. D. and Kravitz, E. A. (2010). Pheromonal and behavioral cues trigger male-to-female aggression in *Drosophila*. *PLoS Biol.* **8**, e1000541.

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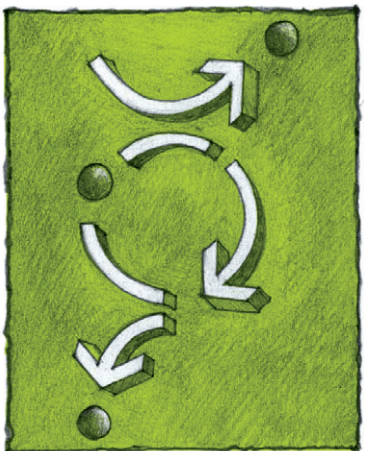
EXERCISE CAPACITY



BAD GENES? KEEP RUNNING!

It doesn't take a trip to the gym to know that we are not all equal in our capacity to exercise. Whether it results from our genes, our environment or both is a source of much debate. The age old question of nature *vs* nurture is certainly central to exercise physiology, notably because of the plasticity of exercise capacity (e.g. training) and the variation of innate traits associated with that capacity.

Sarah Lessard, Donato Rivas and colleagues from Royal Melbourne Institute of Technology University in Australia addressed this question by using rats artificially selected for high or low running capacities. After 22 generations of differential selection, the high-capacity runners exhibit a 5-fold higher running capacity than the low capacity animals. Furthermore, low capacity runners present several metabolic dysfunctions coupled with an impaired health profile that could explain their reduced athleticism. The team's primary hypothesis was that exercise training would reverse some of the metabolic dysfunctions exhibited by the rats selected for low running capacity.

The team trained the two different phenotypes with exercise for 6 weeks and compared the metabolic responses between these two groups and their sedentary matched controls. First, they measured whole body metabolic parameters. Training 'couch-potato' rats lowered their body mass, fat content and serum non-esterified fatty acid levels, suggesting an improvement of their metabolic function. In contrast, the trained 'athletic' rats did not show any significant changes in whole body metabolism, suggesting a *status quo* in metabolic function, at least under the training conditions of the study.

To get a better understanding of the metabolic changes involved with these improvements in low capacity rats, Lessard

and her team investigated glucose and lipid metabolism in isolated skeletal muscle taken from both phenotypes. In agreement with their *in vivo* measurements, muscles of trained low capacity rats showed improvements in both fuel metabolisms compared with their sedentary counterparts. However, exercise training did not affect high capacity runners for any metabolic pathway examined.

Finally, the team looked at the protein levels of metabolic regulators and some of their targets. In sedentary animals, the β-adrenergic receptor and the nuclear receptor Nur77 were both upregulated in the high capacity rats compared with their low capacity counterparts. However, exercise training reduced these differences between the groups by triggering an increase in protein content in low capacity rats but not in high capacity animals. Further, several targets of Nur77 involved in lipid and carbohydrate metabolism (glucose transporter 4, fatty acid translocase CD36 and uncoupling protein 3) all followed a similar pattern. Indeed, these proteins were more abundant in the skeletal muscle of sedentary good runners compared with low capacity rats, but again these differences between the two groups faded following exercise training.

Overall, these results consistently point to an amelioration of the metabolic capacity of 'couch-potato' rats after short-term, low to moderate intensity exercise training. Interestingly, the effects of training were only evident in low capacity animals, with very little impact on the metabolic function of 'good runners'. This probably means that I should really stop blaming my genes and hit the gym!

10.1242/jeb.049650

Lessard, S. J., Rivas, D. A., Stephenson, E. J., Yaspelkis, B. B., 3rd, Koch, L. G., Britton, S. L. and Hawley, J. A. (2011). Exercise training reverses impaired skeletal muscle metabolism induced by artificial selection for low aerobic capacity. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **300**, R175-R182.

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PHENOTYPIC PLASTICITY

SPIDERS HELP GRASSHOPPERS HOP

Living with the constant threat of being eaten is thankfully not something many of us have to deal with, but it is commonplace for many animals. Studies have shown that risky, predator-laden environments tend to lead to physiological stress, but also to prey that are better suited to dealing with their adversaries. In particular, alterations in anatomical traits involved in locomotion and defense arise in populations under the chronic threat of predation. Such phenotypic plasticity is usually quite conspicuous, and as a result has been well studied in a variety of systems, usually aquatic. But what if morphological change isn't the only way to deal with the constant stress of being eaten? Perhaps more nuanced shifts in behavioral strategy are an equally good means of defense or evasion, but have remained under scientists' radars exactly because of their subtlety. This is just the point made in a recent paper by Dror Hawlena, working with Oswald Schmitz and their colleagues at Yale University.

Hawlena and collaborators used grasshoppers as a model for studying subtle biomechanical tactics for enhanced escape performance. This is a good system because earlier work from Schmitz's lab demonstrated that chronic exposure to predatory spiders leads to a physiological stress response in these grasshoppers, but no predator-induced shifts in morphology. Do they exhibit a more highly tuned escape response, despite exhibiting no obvious anatomical changes? To answer this the researchers designed 14 small field plots ($0.25\,m^2$ area$\times$1 m high) and placed six third-instar grasshopper nymphs in each. In seven of the plots, an adult predatory spider was also introduced a day later, although each was rendered harmless with glue holding its chelicerae together. After several months of living in their mesocosms, grasshoppers from spider plots and their controls (no spider ever introduced) were placed into an outdoor, flat arena and stimulated to jump until exhausted. The team recorded jump distances. The animals were then taken into the lab where high-speed video recordings of at least two jumps from each individual were used to calculate variables such as takeoff speed and angle.

In the outdoor experiments grasshoppers raised with spiders jumped, on average, about 50% farther than control animals. Reviewing high-speed videos of lab jumps revealed that the grasshoppers raised in a riskier environment took off at speeds significantly higher than those of animals raised without spiders. Moreover, the former, more skittish animals also appeared to alter the way in which they took off, delaying their onset of motion and improving the tibia's leverage in the 10 ms before takeoff.

Most studies of predator-induced phenotypic plasticity emphasize morphological changes in prey that make them less likely to be eaten, either because of improved defense mechanisms or because of enhanced escape capacity. However, this work demonstrates that species that lack such anatomical alterations can use behavioral or biomechanical shifts to compensate instead. In studying grasshopper jumping in a more ecologically relevant context, Hawlena and colleagues have not only shown that predation threat can improve performance but also provided biomechanists with specific variables related to tibia leverage that deserve more attention in future studies of jumping in these and similar animals.

10.1242/jeb.049684

Hawlena, D., Kress, H., Dufresne, E. R. and Schmitz, O. J. (2010). Grasshoppers alter jumping biomechanics to enhance escape performance under chronic risk of spider predation. *Funct. Ecol.* doi: 10.1111/j.1365-2435.2010.01767.x

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