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Learn. Mem. 2009. 16: 743-750

Circadian rhythms and the evolution of photoperiodic timing in insects
Physiological Entomology Volume 34 Issue 4, Pages 301 – 308 Published Online: 19 Nov 2009
Insect Behaviour

A polyandrous female moth discriminates against previous mates to gain genetic diversity

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Polyandry is common in many animal species. The hypotheses proposed to explain the evolution of polyandry generally fall into two categories: to gain material benefits and to obtain genetic benefits. Here we report our findings on a polyandrous moth, *Ephestia kuehniella* (Lepidoptera: Pyralidae). The present study does not support the hypothesis that females gain material benefits from multiple copulations in terms of sperm replenishment, fecundity and longevity, because females that copulated once and females that copulated more than once with the same or different males had similar fertility, fecundity and longevity. Females used three strategies to gain possible genetic benefits: discriminating against previous mates probably via chemical cues, giving 60% chance of paternity to second males, and adjusting their oviposition patterns depending on whether they encountered new or previous mates after the first copulation. For the third strategy, females that encountered new mates after the first copulation saved eggs until the next day to facilitate fertilization of their eggs with the sperm of their new mates. Our findings do not support the hypothesis that polyandry increases offspring viability, because polyandry did not affect egg hatching success, offspring survival or weight. *Ephestia kuehniella* showed limited ability to disperse, and females laid all their eggs locally, mostly within 2 days, suggesting that offspring live together and that sib copulations are common in this species. Therefore, polyandry is probably a mechanism for reducing sib competition and inbreeding costs in offspring.

Queen replacement in the monogynous ant *Aphaenogaster senilis*: supernumerary queens as life insurance

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In social groups, the replacement of the breeder may generate conflicts. In eusocial hymenoptera these can occur between queens, between queens and workers, or between workers. We investigated queen replacement in the Mediterranean ant *Aphaenogaster senilis*, a monogynous (one queen per colony) species that reproduces exclusively by colony fission. We first investigated the potential for worker nepotism by analysing the sociogenetic structure in 31 colonies using microsatellite markers. No polyandry was detected, which eliminates the possibility of worker nepotism. Second, 30 colonies were experimentally orphaned to analyse the production of gynes (unmated, hopeful queens). Workers reared on average two gynes from the previous queen's diploid brood, with the firstborn gyne emerging on average 17 days before the other, supernumerary, gyne(s). The production of only a few gynes severely limits the potential for gyne selection based on quality criteria. Furthermore, such selection would be biased by the asynchrony of gyne emergence which precludes comparing gynes of the same age and maturity. Behavioural observations showed that gynes interacted aggressively and that the firstborn gyne was always dominant. She usually survived while supernumerary gynes seldom did, even though they did not differ in weight. Workers also attacked gynes, and preferentially targeted supernumerary gynes. We propose that supernumerary gynes are produced as insurance in the eventuality of the death of the firstborn gyne, and that the
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delay between the emergence of gynes minimizes the risk that aggressive interactions between gynes will lead to all gynes being killed.

Sexual selection for genetic quality: disentangling the roles of male and female behaviour

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According to the good genes model of sexual selection, females choose males of good heritable genetic quality to obtain offspring with high fitness. However, better mating success of high-quality males can also be brought about by direct interference competition between males, or simply through elevated activity of high-quality males. We examined the roles of different processes leading to sexual selection for genetic quality in Drosophila montana. We manipulated genetic quality of male flies by inducing mutations with ionizing radiation. We then recorded the effects of inherited heterozygous mutations on several aspects of mating behaviour of males and females in two experiments. We found that mutations reduced the probability of courtship and extended the latency to courtship of the males, suggesting male activity plays a role in selection for genetic quality. However, the effects of mutations on mating success and mating behaviour of the flies were in general weak. No evidence for female mate choice or interference competition between males acting against heritable mutations was found.

Policing and dominance behaviour in the parthenogenetic ant Platythyrea punctata

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In the parthenogenetic ant Platythyrea punctata policing behaviour is not expected on relatedness grounds as workers are normally clonemates and thus equally related to all offspring in the colony. Nevertheless, colonies usually contain only a single reproductive and other workers that begin to lay eggs are attacked by their nestmates (‘policing’). We found that those individuals that most actively engaged in policing later themselves had activated ovaries when the old reproductive was removed from the colonies. This suggests that police workers, through attacking and eliminating others, increase their own chances of becoming reproductive themselves. Because regular parthenogenesis leads to a clonal colony structure, individuals are not expected to invest energy in dominance and policing. On the assumption that physical dominance reflects an individual’s reproductive potential, aggression among workers might ensure that the most fecund individual becomes the next reproductive, which would benefit the colony as a whole. Furthermore, aggression among nestmates may be maintained in this species despite predominant clonality, because infrequent sex, recombination or the adoption of alien workers may introduce genetic heterogeneity into the colony.
Unexpected absence of behavioural differences between female damselfly colour morphs

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Males are often selected for higher mating rates than females. As a consequence of this sexual conflict, unreceptive females may suffer fitness costs from excessive male sexual harassment. In a variety of vertebrate and invertebrate species, multiple female morphs coexist in natural populations which have been observed to differ in body colour, in behaviour and also in the amount of male harassment received. However, the degree of harassment on a female morph may depend on the frequency and density of males and female morphs in the population. We quantified harassment rate and subsequent refusal behaviour of males and female morphs of the polymorphic damselfly Nehalennia irene. Unexpectedly and contrary to previous work, female morphs received similar amounts of male harassment and showed mostly the same behaviour. We discuss why differences in morph behaviours may be lacking and how this compares to contemporary explanations for the maintenance and evolution of female-limited polymorphisms.

Homosexual interactions in bed bugs: alarm pheromones as male recognition signals

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Homosexual mounting is a common behaviour in bed bugs as male sexual interest is directed towards any newly fed individual. The only mode of copulation in the common bed bug, Cimex lectularius, is by traumatic insemination, where the male pierces the female abdomen with his needle-like penis. Homosexual mating would result in abdominal injuries in mounted males, as males lack the female counteradaptive spermalege structure. I here show that bed bug alarm pheromones, previously hypothesized to be a predator chemical defence, can be used by newly fed males to signal their sex and reduce the risk of homosexual mating. Mechanical blocking of the male pheromone glands significantly increased homosexual mounting duration compared to control males, while applying male extracts containing mainly alarm pheromone onto male–female mating pairs completely interrupted or shortened mating duration and reduced sperm transfer. Males confined with other males received piercing scars, demonstrating that homosexual mating occurs. The focal males in the all-male confinement experiment had reduced longevity compared to singly held males, but why this reduction in longevity occurred is not clear. Mounted males thus benefit from being able to discharge alarm pheromones, while mounting males consider the alarm signal a major sex identification cue, suggesting that male bed bugs use alarm pheromone communication to avoid homosexual harassment and mounting.

Preimaginal and Adult Experience Modulates the Thermal Response Behavior of Ants

Anja Weidenmüller, Christina Mayr, Christoph Johannes Kleineidam and Flavio Roces
Colonies of social insects display an amazing degree of flexibility in dealing with long-term and short-term perturbations in their environment. The key organizational element of insect societies is division of labor. Recent literature suggests that interindividual variability in response thresholds plays an important role in the emergence of division of labor among workers (reviewed in [1,2]). Genetic variation can only partly explain the variability among workers. Here we document the effects of both preimaginal and adult thermal experience on the behavioral differentiation of *Camponotus rufipes* ant workers. We show that preimaginal temperature (22°C or 32°C during pupal stage) affects temperature-response thresholds and temperature preferences of adult brood-tending workers. We further show that brood-carrying experience gathered as adult during several repeated temperature increases modifies thermal behavior. Experienced workers showed a faster transition from first sensing the temperature stimulus to responding with brood translocation. Developmental plasticity of workers provides a colony with flexibility in dealing with thermal variations and constitutes an important mechanism underlying interindividual variability. Adult thermal experience further fine tunes the behavioral response thresholds and reinforces behavioral differentiation among workers.

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http://www.cell.com/current-biology/abstract/S0960-9822%2809%2901760-6

**Insect Cell Biology**

**Increased Cell Bond Tension Governs Cell Sorting at the *Drosophila* Anteroposterior Compartment Boundary**

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Subdividing proliferating tissues into compartments is an evolutionarily conserved strategy of animal development [1,2,3,4,5,6]. Signals across boundaries between compartments can result in local expression of secreted proteins organizing growth and patterning of tissues [1,2,3,4,5,6]. Sharp and straight interfaces between compartments are crucial for stabilizing the position of such organizers and therefore for precise implementation of body plans. Maintaining boundaries in proliferating tissues requires mechanisms to counteract cell rearrangements caused by cell division; however, the nature of such mechanisms remains unclear. Here we quantitatively analyzed cell morphology and the response to the laser ablation of cell bonds in the vicinity of the anteroposterior compartment boundary in developing *Drosophila* wings. We found that mechanical tension is approximately 2.5-fold increased on cell bonds along this compartment boundary as compared to the remaining tissue. Cell bond tension is decreased in the presence of Y-27632 [7], an inhibitor of Rho-kinase whose main effector is Myosin II [8]. Simulations using a vertex model [9] demonstrate that a 2.5-fold increase in local cell bond tension suffices to guide the rearrangement of cells after cell division to maintain compartment boundaries. Our results provide a physical mechanism in which the local increase in Myosin II-dependent cell bond tension directs cell sorting at compartment boundaries.

http://www.cell.com/current-biology/abstract/S0960-9822%2809%2901840-5
Insect Cellular Metabolism

Schlank, a member of the ceramide synthase family controls growth and body fat in *Drosophila*

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Ceramide synthases are highly conserved transmembrane proteins involved in the biosynthesis of sphingolipids, which are essential structural components of eukaryotic membranes and can act as second messengers regulating tissue homeostasis. However, the role of these enzymes in development is poorly understood due to the lack of animal models. We identified *schlank* as a new *Drosophila* member of the ceramide synthase family. We demonstrate that schlank is involved in the *de novo* synthesis of a broad range of ceramides, the key metabolites of sphingolipid biosynthesis. Unexpectedly, schlank mutants also show reduction of storage fat, which is deposited as triacylglycerols in the fat body. We found that schlank can positively regulate fatty acid synthesis by promoting the expression of sterol-responsive element-binding protein (SREBP) and SREBP-target genes. It further prevents lipolysis by downregulating the expression of triacylglycerol lipase. Our results identify schlank as a new regulator of the balance between lipogenesis and lipolysis in *Drosophila*. Furthermore, our studies of schlank and the mammalian Lass2 family member suggest a novel role for ceramide synthases in regulating body fat metabolism.

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http://www.nature.com/emboj/journal/v28/n23/abs/emboj2009305a.html

Insect Chemoecology

Molecular Characterization and Expression Pattern of Two General Odorant Binding Proteins from the Diamondback Moth, *Plutella xylostella*

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In the Lepidoptera, odorant signals are thought to be mediated by general odorant binding proteins (GOBPs) in the sensillar lymph surrounding the olfactory receptors. We describe the identification and characterization of two new cDNAs encoding GOBPs from the antennae of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), a species for which no GOBPs have been identified to date. We focused our investigation on this olfactory protein family by using reverse transcription–polymerase chain reaction strategies. The deduced amino acid sequences of PxylGOBP1 and PxylGOBP2 revealed open reading frames of 168 and 163 amino acids, respectively, with six cysteine residues in conserved positions relative to other known GOBPs. The alignment of the mature PxylGOBPs with other Lepidoptera GOBPs showed high sequence identity (70–80%) with other full-length sequences from GenBank. Sequence identity between PxylGOBP1 and PxylGOBP2 was only 50%, suggesting that the two proteins belong to different classes of lepidopteran GOBPs. The expression patterns of the two PxylGOBP genes, with respect to tissue distribution and sex, were further investigated by reverse transcription-polymerase chain reaction (RT-PCR) and real-time PCR. Although the two GOBP genes were expressed only in the antennae of both sexes, reflecting the antennal specificity of GOBPs,
Plants under herbivore attack are able to initiate indirect defense by synthesizing and releasing complex blends of volatiles that attract natural enemies of the herbivore. However, little is known about how plants respond to infestation by multiple herbivores, particularly if these belong to different feeding guilds. Here, we report the interference by a phloem-feeding insect, the whitefly Bemisia tabaci, with indirect plant defenses induced by spider mites (Tetranychus urticae) in Lima bean (Phaseolus lunatus) plants. Additional whitefly infestation of spider-mite infested plants resulted in a reduced attraction of predatory mites (Phytoseiulus persimilis) compared to attraction to plants infested by spider mites only. This interference is shown to result from the reduction in (E)-β-ocimene emission from plants infested by both spider mites and whiteflies. When using exogenous salicylic acid (SA) application to mimic B. tabaci infestation, we observed similar results in behavioral and chemical analyses. Phytohormone and gene-expression analyses revealed that B. tabaci infestation, as well as SA application, inhibited spider mite-induced jasmonic acid (JA) production and reduced the expression of two JA-regulated genes, one of which encodes for the P. lunatus enzyme β-ocimene synthase that catalyzes the synthesis of (E)-β-ocimene. Remarkably, B. tabaci infestation concurrently inhibited SA production induced by spider mites. We therefore conclude that in dual-infested Lima bean plants the suppression of the JA signaling pathway by whitefly feeding is not due to enhanced SA levels.
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CRY. On the basis of our findings, we propose that CRY can gate PDF signaling to determine behavioral phase and network hierarchy.

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Insect Development

Function of Drosophila mob2 in photoreceptor morphogenesis

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The Drosophila photoreceptor is a highly polarized cell; a mature photoreceptor cell in Drosophila contains a photosensitive structure (the rhabdomere) and a supporting membrane (stalk) at its apical membrane. In a screen to isolate genes involved in determining stalk and rhabdomere formation, this study has identified the Drosophila mob2 (Dmob2) gene. Dmob2 belongs to a Mob1/phocein domain protein family whose functions are involved in polarized cell growth and asymmetric cell fate determination in yeast. To study the role of Dmob2 in photoreceptor development, we have raised an antibody against the Dmob2 protein. An immunocytochemical study has shown that Dmob2 is mainly localized in the apical membrane of photoreceptor cells during early development. As development proceeds, Dmob2 is gradually confined to the rhabdomere base of the photoreceptor cells. RNA interference (RNAi) for knockdown Dmob2 expression during eye development impairs rhabdomere formation. Our study further shows that the subcellular localization of phosphorylated Moesin and Crumbs in the developing photoreceptor cell is disrupted in Dmob2 RNAi flies. This work thus reports a novel function of Dmob2 in photoreceptor cell development.

http://www.springerlink.com/content/6271281k45685307/

Visualization of Individual Scr mRNAs during Drosophila Embryogenesis Yields Evidence for Transcriptional Bursting

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The detection and counting of transcripts within single cells via fluorescent in situ hybridization (FISH) [1,2,3,4,5,6] has allowed researchers to ask quantitative questions about gene expression at the level of individual cells. This method is often preferable to quantitative RT-PCR [7,8,9], because it does not necessitate destruction of the cells being probed and maintains spatial information that may be of interest. Until now, studies using FISH at single-molecule resolution have only been rigorously carried out in isolated cells (e.g., yeast cells or mammalian cell culture). Here, we describe the detection and counting of transcripts within single cells of fixed, whole-mount Drosophila embryos via a combination of FISH, immunohistochemistry, and image segmentation. Our method takes advantage of inexpensive, long RNA probes detected with antibodies [10,11], and we present novel evidence to show that we can robustly detect single mRNA molecules. We use this method to characterize transcription at the endogenous locus of the Hox gene Sex combs reduced (Scr), by comparing a stably expressing group of cells to a group that only transiently expresses the gene. Our data provide evidence for
transcriptional bursting [2,5,12,13,14,15,16], as well for divergent “accumulation” and “maintenance” phases of gene activity at the Scr locus.

Insect Ecology

Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology

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Climatically driven Moran effects have often been invoked as the most likely cause of regionally synchronized outbreaks of insect herbivores without identifying the exact mechanism. However, the degree of match between host plant and larval phenology is crucial for the growth and survival of many spring-feeding pest insects, suggesting that a phenological match/mismatch-driven Moran effect may act as a synchronizing agent. We analyse the phase-dependent spatial dynamics of defoliation caused by cyclically outbreaking geometrid moths in northern boreal birch forest in Fennoscandia through the most recent massive outbreak (2000–2008). We use satellite-derived time series of the prevalence of moth defoliation and the onset of the growing season for the entire region to investigate the link between the patterns of defoliation and outbreak spread. In addition, we examine whether a phase-dependent coherence in the pattern of spatial synchrony exists between defoliation and onset of the growing season, in order to evaluate if the degree of matching phenology between the moth and their host plant could be the mechanism behind a Moran effect.
The strength of regional spatial synchrony in defoliation and the pattern of defoliation spread were both highly phase-dependent. The incipient phase of the outbreak was characterized by high regional synchrony in defoliation and long spread distances, compared with the epidemic and crash phase. Defoliation spread was best described using a two-scale stratified spread model, suggesting that defoliation spread is governed by two processes operating at different spatial scale. The pattern of phase-dependent spatial synchrony was coherent in both defoliation and onset of the growing season. This suggests that the timing of spring phenology plays a role in the large-scale synchronization of birch forest moth outbreaks.

http://rspb.royalsocietypublishing.org/content/276/1676/4119.abstract

Insect Evolution

EFFECTS OF PARTHENOGENESIS AND GEOGRAPHIC ISOLATION ON FEMALE SEXUAL TRAITS IN A PARASITOID WASP

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Population divergence in sexual traits is affected by different selection pressures, depending on the mode of reproduction. In allopatric sexual populations, aspects of sexual behavior may diverge due to sexual selection. In parthenogenetic populations, loss-of-function mutations in genes involved in sexual functionality may be selectively neutral or favored by selection. We assess to what extent these processes have contributed to divergence in female sexual traits in the parasitoid wasp Leptopilina clavipes in which some populations are infected with parthenogenesis-inducing Wolbachia bacteria. We find evidence consistent with both hypotheses. Both arrhenotokous males and males derived from thelytokous strains preferred to court females from their own population. This suggests that these populations had already evolved population-specific mating preferences when the latter became parthenogenetic. Thelytokous females did not store sperm efficiently and fertilized very few of their eggs. The nonfertility of thelytokous females was due to mutations in the wasp genome, which must be an effect of mutation accumulation under thelytoky. Divergence in female sexual traits of these two allopatric populations has thus been molded by different forces: independent male/female coevolution while both populations were still sexual, followed by female-only evolution after one population switched to parthenogenesis.

http://www3.interscience.wiley.com/journal/122526547/abstract

THE TEMPO AND MODE OF EVOLUTION OF TRANSPposables ELEMENTS AS REVEALED BY MOLECULAR PHYLOGENIES RECONSTRUCTED FROM MOSQUITO GENOMES

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Although many mathematical models exist predicting the dynamics of transposable elements (TEs), there is a lack of available empirical data to validate these models and inherent assumptions. Genomes can provide a snapshot of several TE families in a single organism, and these could have their demographics inferred by coalescent analysis, allowing for the testing of theories on TE amplification dynamics. Using the available
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Genomes of the mosquitoes *Aedes aegypti* and *Anopheles gambiae*, we indicate that such an approach is feasible. Our analysis follows four steps: (1) mining the two mosquito genomes currently available in search of TE families; (2) fitting, to selected families found in (1), a phylogeny tree under the general time-reversible (GTR) nucleotide substitution model with an uncorrelated lognormal (UCLN) relaxed clock and a nonparametric demographic model; (3) fitting a nonparametric coalescent model to the tree generated in (2); and (4) fitting parametric models motivated by ecological theories to the curve generated in (3).

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http://www3.interscience.wiley.com/journal/122523803/abstract

**EVOLUTION OF IDENTITY SIGNALS: FREQUENCY-DEPENDENT BENEFITS OF DISTINCTIVE PHENOTYPES USED FOR INDIVIDUAL RECOGNITION**

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Identifying broad-scale evolutionary processes that maintain phenotypic polymorphisms has been a major goal of modern evolutionary biology. There are numerous mechanisms, such as negative frequency-dependent selection, that may maintain polymorphisms, although it is unknown which mechanisms are prominent in nature. Traits used for individual recognition are strikingly variable and have evolved independently in numerous lineages, providing an excellent model to investigate which factors maintain ecologically relevant phenotypic polymorphisms. Theoretical models suggest that individuals may benefit by advertising their identities with distinctive, recognizable phenotypes. Here, we test the benefits of advertising one's identity with a distinctive phenotype. We manipulated the appearance of *Polistes fuscatus* paper wasp groups so that three individuals had the same appearance and one individual had a unique, easily recognizable appearance. We found that individuals with distinctive appearances received less aggression than individuals with nondistinctive appearances. Therefore, individuals benefit by advertising their identity with a unique phenotype. Our results provide a potential mechanism through which negative frequency-dependent selection may maintain the polymorphic identity signals in *P. fuscatus*. Given that recognition is important for many social interactions, selection for distinctive identity signals may be an underappreciated and widespread mechanism underlying the evolution of phenotypic polymorphisms in social taxa.

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http://www3.interscience.wiley.com/journal/122594183/abstract

**Bacterial gut symbionts are tightly linked with the evolution of herbivory in ants**

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Ants are a dominant feature of terrestrial ecosystems, yet we know little about the forces that drive their evolution. Recent findings illustrate that their diets range from herbivorous to predaceous, with "herbivores" feeding primarily on exudates from plants and sap-feeding insects. Persistence on these nitrogen-poor food sources raises the question of how ants obtain sufficient nutrition. To investigate the potential role of
symbiotic microbes, we have surveyed 283 species from 18 of the 21 ant subfamilies using molecular techniques. Our findings uncovered a wealth of bacteria from across the ants. Notable among the surveyed hosts were herbivorous “turtle ants” from the related genera Cephalotes and Procyrtocerus (tribe Cephalotini). These commonly harbored bacteria from ant-specific clades within the Burkholderiales, Pseudomonadales, Rhizobiales, Verrucomicrobiales, and Xanthomonadales, and studies of lab-reared Cephalotes varians characterized these microbes as symbiotic residents of ant guts. Although most of these symbionts were confined to turtle ants, bacteria from an ant-specific clade of Rhizobiales were more broadly distributed. Statistical analyses revealed a strong relationship between herbivory and the prevalence of Rhizobiales gut symbionts within ant genera. Furthermore, a consideration of the ant phylogeny identified at least five independent origins of symbioses between herbivorous ants and related Rhizobiales. Combined with previous findings and the potential for symbiotic nitrogen fixation, our results strongly support the hypothesis that bacteria have facilitated convergent evolution of herbivory across the ants, further implicating symbiosis as a major force in ant evolution.

PNAS December 15, 2009 vol. 106 no. 50 21236-21241
http://www.pnas.org/content/106/50/21236.abstract?etoc

Insect Genetics

Little Effect of the tan Locus on Pigmentation in Female Hybrids between Drosophila santomea and D. melanogaster

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Previous work on Drosophila santomea suggested that its absence of abdominal pigmentation, compared to the other darkly pigmented species, is based on mutations in the cis-regulatory region of tan, inactivating the expression of that gene in the abdomen of D. santomea males and females. Our discovery that D. santomea males can produce viable hybrids when mated to D. melanogaster females enables us to use the armamentarium of genetic tools in the latter species to study the genetic basis of this interspecific difference in pigmentation. Hybridization tests using D. melanogaster deficiencies that include tan show no evidence that this locus is involved in the lighter pigmentation of D. santomea females; rather, the pigmentation difference appears to involve at least four other loci in the region. Earlier results implicating tan may have been based on a type of transgenic analysis that can give misleading results about the genes involved in an evolutionary change.

Cell, Volume 139, Issue 6, 1180-1188, 11 December 2009
http://www.cell.com/abstract/S0092-8674%2809%2901359-2

Evolution of the tan Locus Contributed to Pigment Loss in Drosophila santomea: A Response to Matute et al.

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We have shown previously that the loss of abdominal pigmentation in *D. santomea* relative to its sister species *D. yakuba* resulted, in part, from cis-regulatory mutations at the tan locus. Matute et al. claim, based solely upon extrapolation from genetic crosses of *D. santomea* and *D. melanogaster*, a much more divergent species, that at least four X chromosome regions but not tan are responsible for pigmentation differences. Here, we provide additional evidence from introgressions of *D. yakuba* genes into *D. santomea* that support a causative role for tan in the loss of pigmentation and present analyses that contradict Matute et al.’s claims. We discuss how the choice of parental species and other factors affect the ability to identify loci responsible for species divergence, and we affirm that all of our previously reported results and conclusions stand.

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**X-Linked Variation in Immune Response in *Drosophila melanogaster***

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This study quantifies the effects of naturally occurring X-linked variation on immune response in *Drosophila melanogaster* to assess associations between immunity genotypes and innate immune response. We constructed a set of 168 X-chromosomal extraction lines, incorporating X chromosomes from a natural population into co-isogenic autosomal backgrounds, and genotyped the lines at 88 SNPs in 20 X-linked immune genes. We find that genetic variation in many of the genes is associated with immune response phenotypes, including bacterial load and immune gene expression. Many of the associations act in a sex-specific or sexually antagonistic manner, supporting the theory that with the selective pressures facing genes on the X chromosome, sexually antagonistic variation may be more easily maintained.

Genetics, Vol. 183, 1477-1491, December 2009
http://www.genetics.org/cgi/content/abstract/183/4/1477?etoc

**Altered Heterochromatin Binding by a Hybrid Sterility Protein in *Drosophila* Sibling Species**

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Hybrid sterility of the heterogametic sex is one of the first postzygotic reproductive barriers to evolve during speciation, yet the molecular basis of hybrid sterility is poorly understood. We show that the hybrid male sterility gene *Odysseus-site homeobox (OdsH)* encodes a protein that localizes to evolutionarily dynamic loci within heterochromatin and leads to their decondensation. In *Drosophila mauritiana x Drosophila simulans* male hybrids, OdsH from *D. mauritiana* (OdsHmau) acts as a sterilizing factor by associating with the heterochromatic Y chromosome of *D. simulans*, whereas *D. simulans* OdsH (OdsHsim) does not. Characterization of sterile hybrid testes revealed that OdsH abundance and localization in the premeiotic phases of spermatogenesis differ between species. These results reveal that rapid heterochromatin evolution affects the onset of hybrid sterility.

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http://www.sciencemag.org/cgi/content/abstract/326/5959/1538?sa_campaign=Email/toc/11-December-2009/10.1126/science.1181756
Insect Hearing

The cost of assuming the life history of a host: acoustic startle in the parasitoid fly *Ormia ochracea*

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In the obligatory reproductive dependence of a parasite on its host, the parasite must trade the benefit of ‘outsourcing’ functions like reproduction for the risk of assuming hazards associated with the host. In the present study, we report behavioral adaptations of a parasitic fly, *Ormia ochracea*, that resemble those of its cricket hosts. *Ormia* females home in on the male cricket’s songs and deposit larvae, which burrow into the cricket, feed and emerge to pupate. Because male crickets call at night, gravid female *Ormia* in search of hosts are subject to bat predation, in much the same way as female crickets are when responding to male song. We show that *Ormia* has evolved the same evasive behavior as have crickets: an acoustic startle response to bat-like ultrasound that manifests clearly only during flight. Furthermore, like crickets, *Ormia* has a sharp response boundary between the frequencies of song and bat cries, resembling categorical perception first described in the context of human speech.


http://jeb.biologists.org/cgi/content/abstract/212/24/4056?etoc

Moths are not silent, but whisper ultrasonic courtship songs

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Ultrasonic hearing is widespread among moths, but very few moth species have been reported to produce ultrasounds for sexual communication. In those that do, the signals are intense and thus well matched for long distance communication. By contrast, males of the Asian corn borer moth (Crambidae) were recently shown to whisper extremely low-intensity ultrasonic courtship songs close to females. Since low sound levels will prevent eavesdropping by predators, parasites and conspecific rivals, we predicted low intensity ultrasound communication to be widespread among moths. Here we tested 13 species of moths including members of the Noctuidae, Arctiidae, Geometridae and Crambidae. Males of nine species, 70%, produced broadband ultrasound close to females. Peak frequencies ranged from 38 to above 100 kHz. All sounds were of low intensity, 43-76 dB SPL at 1 cm [64±10 dB peSPL (mean ± s.d.), \(N=9\) species]. These quiet and/or hyper-frequency ultrasounds are audible to nearby mates, but inaudible to unintended receivers. Although largely unknown because it is so inconspicuous, acoustic communication using low intensity ultrasound appears to be widespread among hearing moths. Thus, acoustic communication may be the norm rather than the exception.

Key words: acoustic communication, courtship behavior, low sound level, moths, ultrasound

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Female cicadas use sound when they select a mate from a chorus of singing males. The cicada has a tympanal ear; and the tympanal membrane, and constituent tympanal ridge, act as both acousto-mechanical transducers and frequency filters. The tympanal ridge is physically connected to a large number of mechanoreceptor neurons via a cuticular extension known as the tympanal apodeme. Using microscanning laser Doppler vibrometry, we measured for the first time the in vivo vibrations of the apodeme of female Cicadatra atra in response to the motion of the tympanum driven by sound. These measurements reveal that the nanoscale motion of the tympanal membrane is over a magnitude greater than that of the apodeme. Furthermore, the apodeme acts as an additional mechanical frequency filter, enhancing that of the tympanal ridge, narrowing the frequency band of vibration at the mechanoreceptor neurons to that of the male calling song. This study enhances our understanding of the mechanical link between the external ear of the cicada and its sensory cells.

http://jeb.biologists.org/cgi/content/abstract/212/24/4079?etoc

Acoustical mimicry in a predatory social parasite of ants

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Rapid, effective communication between colony members is a key attribute that enables ants to live in dominant, fiercely protected societies. Their signals, however, may be mimicked by other insects that coexist as commensals with ants or interact with them as mutualists or social parasites. We consider the role of acoustics in ant communication and its exploitation by social parasites. Social parasitism has been studied mainly in the butterfly genus Maculinea, the final instar larvae of which are host-specific parasites of Myrmica ants, preying either on ant grubs (predatory Maculinea) or being fed by trophallaxis (cuckoo Maculinea). We found similar significant differences between the stridulations of model queen and worker ant castes in both Myrmica sabuleti and Myrmica scabrinodis to that previously reported for Myrmica schencki. However, the sounds made by queens of all three Myrmica species were indistinguishable, and among workers, stridulations did not differ significantly in two of three species-pairs tested. Sounds recorded from the predatory caterpillars and pupae of Maculinea arion had similar or closer patterns to the acoustics of their host Myrmica sabuleti than those previously reported for the cuckoo Maculinea rebellii and its host Myrmica schencki, even though Maculinea rebellii caterpillars live more intimately with their host. We conclude that chemical mimicry enables Maculinea larvae to be accepted as colony members by worker ants, but that caterpillars and pupae of both predatory and cuckoo butterflies employ acoustical mimicry of queen ant calls to elevate their status towards the highest attainable position within their host’s social hierarchy.

http://jeb.biologists.org/cgi/content/abstract/212/24/4084?etoc

Evaluation of amplitude in male song: female waxmoths respond to fortissimo notes
Female evaluation of male signals in the context of sexual selection is often made on the basis of signal energy. Particularly in acoustic species, females may prefer male song that is broadcast at greater amplitude or power. However, song amplitude may be represented by various parameters, and the specific one(s) that are evaluated are not clear. We addressed this problem in an acoustic moth, *Achroia grisella* (Lepidoptera: Pyralidae), where males attract females with trains of paired ultrasonic pulses. Previous studies showed that females prefer songs that include pulse pairs that have greater mean peak amplitude and that are delivered with greater power (=mean peak amplitude × pulse-pair rate). Here, we report that given male songs of equal acoustic power, females prefer songs in which some pulses attain peak amplitudes that exceed the mean value and that this preference depends largely on the magnitude of amplitude fluctuation. We measured significant variation among males in their degree of amplitude fluctuation, and we note that males that broadcast with lower acoustic power typically show greater relative fluctuations and attain relatively higher amplitude maxima. We discuss the potential role of multiple integration time constants in female evaluation of mean song amplitude and amplitude maxima. We then consider the possibility that the variation observed in the male population is a response to female choice, but we also indicate that mechanical factors constraining song production may be responsible for such variation.

http://jeb.biologists.org/cgi/content/abstract/212/24/4084?etoc

**Interspecific and intersexual learning rate differences in four butterfly species**

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Learning plays an important role in food acquisition for a wide range of insects and has been demonstrated to be essential during flower foraging in taxa such as bees, parasitoid wasps, butterflies and moths. However, little attention has been focused on differences in floral cue learning abilities among species and sexes. We examined the associative learning of flower colour with nectar in four butterfly species: *Idea leuconoe, Argyreus hyperbius, Pieris rapae and Lycaena phlaeas*. All butterflies that were trained learned the flower colours associated with food. The flower colour learning rates were significantly higher in *I. leuconoe* and *A. hyperbius* than in *P. rapae* and L. phlaeas. Among the four species examined, the larger and longer-lived species exhibited higher learning rates. Furthermore, female butterflies showed a significantly higher learning rate than males. This study provides the first evidence that learning abilities related to floral cues differ among butterfly species. The adaptive significance of superior learning abilities in the larger and longer-lived butterfly species and in females is discussed.

http://jeb.biologists.org/cgi/content/abstract/212/23/3810?etoc

**Thermal learning in the honeybee, Apis mellifera**

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[Image 71x767 to 163x807]
Honeybee foragers are exposed to thermal stimuli when collecting food outside and receiving food rewards inside the nest. In both contexts, there is an opportunity for foragers to associate warmth with food rewards. However, honeybee thermal learning is poorly understood. Using an associative learning paradigm (the proboscis extension reflex), we show that honeybees can learn to associate a nectar reward with a heated stimulus applied to the antenna to mimic natural contact with a warm flower or nectar-offering forager. Conditioning with longer inter-trial intervals (ITI) significantly improved learning acquisition. We also trained bees to discriminate between temperatures above (warm) and below (cold) ambient air temperature. Learning acquisition improved by 38% per 10°C increase in absolute stimulus intensity (difference between the rewarded temperature and unrewarded ambient air temperature). However, bees learned positive temperature (warm) significantly better than negative temperature (cold) differences, approximately twice as well for 10°C as compared with a –10°C difference. Thus, thermosensation, a sensory modality that is relatively unexplored in honeybees, could play a role in the acquisition of information from nestmates (social learning) and in foraging decisions influenced by associations between floral temperature and nectar rewards.

http://jeb.biologists.org/cgi/content/abstract/212/23/3928?etoc

Structural and proteomic analyses reveal regional brain differences during honeybee aging

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Among insects, learning is particularly well studied in the fruit fly Drosophila melanogaster and the honeybee Apis mellifera. A senescence-dependent decline in classic pavlovian conditioning is demonstrated for both species. To understand how aging affects learning, genetic approaches used with Drosophila can benefit from complementary studies in Apis. Specifically, honeybees have a larger brain size allowing for compartment-specific approaches, and a unique life-history plasticity. They usually perform within-nest tasks early in life (nest bees) and later they collect food (foragers). Senescence of learning performance is a function of the bees’ foraging duration but underlying causes are poorly understood. As cognitive aging is commonly associated with structural and biochemical changes in the brain, we hypothesized that brain areas implicated in learning change in synaptic and biochemical composition with increased foraging duration. First, we used synapse-specific immunohistochemistry and proteomics to screen for alterations in the calyx region of the mushroom body, a key structure for memory formation. Using proteomics, we next profiled the central brain, which comprises all higher-order integration centers. We show that, with increased foraging duration, levels of kinases, synaptic- and neuronal growth-related proteins decline in the central brain while the calyx region remains intact both in structure and biochemistry. We suggest that proteome-level changes within major anatomical sites of memory formation other than the calyx region could be central to learning dysfunction. These include large compartments of the central brain, such as the mushroom body's output regions and the antennal lobes. Our data provide novel information toward heterogeneity in the aging insect brain, and demonstrate advantages of the honeybee for invertebrate neurogerontological research.

http://jeb.biologists.org/cgi/content/abstract/212/24/4027
Olfactory conditioning of the sting extension reflex in honeybees: Memory dependence on trial number, interstimulus interval, intertrial interval, and protein synthesis

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Harnessed bees learn to associate an odorant with an electric shock so that afterward the odorant alone elicits the sting extension response (SER). We studied the dependency of retention on interstimulus interval (ISI), intertrial interval (ITI), and number of conditioning trials in the framework of olfactory SER conditioning. Forward ISIs (conditioned stimulus [CS] before unconditioned stimulus [US]) supported higher retention than a backward one (US before CS) with an optimum around 3 sec. Spaced trials (ITI 10 min) supported higher retention than massed trials (ITI 1 min) and led to the formation of a late long-term memory (l-LTM) that depended on protein synthesis. Our results reaffirm olfactory SER conditioning as a reliable tool for the study of learning and memory.

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http://learnmem.cshlp.org/content/16/12/761.abstract

Social learning about egg-laying substrates in fruitflies

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Social learning, defined as learning from other individuals, has had dramatic effects on some species, including humans, in whom it has generated a rich culture. As a first step in examining the evolution of and mechanisms underlying social learning in insects, we tested for social learning in fruitflies (Drosophila melanogaster). Focal females (observers) that experienced novel food together with mated females (models), who had laid eggs on that food, subsequently exhibited a stronger preference for laying eggs on that food over another novel food compared with focal females that experienced the food alone. We observed no social learning, however, when observers experienced food with potentially more ambiguous social information provided by the presence of either virgin models or aggregation pheromone. This first documentation of social learning about egg-laying substrates in fruitflies builds on recent data indicating intricate use of social information by fruitflies and opens up exciting avenues for research on the evolution and neurogenetics of social learning using biology's major model system.

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Insect Metamorphosis

The Insect Neuropeptide PTTH Activates Receptor Tyrosine Kinase Torso to Initiate Metamorphosis

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Holometabolous insects undergo complete metamorphosis to become sexually mature adults. Metamorphosis is initiated by brain-derived prothoracotrophic hormone (PTTH), which stimulates the production of the molting hormone ecdysone via an incompletely defined signaling pathway. Here we demonstrate that Torso, a receptor tyrosine kinase that regulates embryonic terminal cell fate in *Drosophila*, is the PTTH receptor. Trunk, the embryonic Torso ligand, is related to PTTH, and ectopic expression of PTTH in the embryo partially rescues trunk mutants. In larvae, torso is expressed specifically in the prothoracic gland (PG), and its loss phenocopies the removal of PTTH. The activation of Torso by PTTH stimulates extracellular signal–regulated kinase (ERK) phosphorylation, and the loss of ERK in the PG phenocopies the loss of PTTH and Torso. We conclude that PTTH initiates metamorphosis by activation of the Torso/ERK pathway.

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c/4-December-2009/10.1126/science.1176450

Insect Molecular Biology

**Functional involvement of Tudor and dPRMT5 in the piRNA processing pathway in *Drosophila* germlines**

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In *Drosophila*, the PIWI proteins, Aubergine (Aub), AGO3, and Piwi are expressed in germlines and function in silencing transposons by associating with PIWI-interacting RNAs (piRNAs). Recent studies show that PIWI proteins contain symmetric dimethyl-arginines (sDMAs) and that dPRMT5/Capsuleen/DART5 is the modifying enzyme. Here, we show that Tudor (Tud), one of Tud domain-containing proteins, associates with Aub and AGO3, specifically through their sDMA modifications and that these three proteins form heteromeric complexes. piRNA precursor-like molecules are detected in these complexes. The expression levels of Aub and AGO3, along with their degree of sDMA modification, were not changed by tud mutations. However, the population of transposon-derived piRNAs associated with Aub and AGO3 was altered by tud mutations, whereas the total amounts of small RNAs on Aub and AGO3 was increased. Loss of dprmt5 did not change the stability of Aub, but impaired its association with Tud and lowered piRNA association with Aub. Thus, in germline cells, piRNAs are quality-controlled by dPRMT5 that modifies PIWI proteins, in tight association with Tud.

The EMBO Journal (2009) 28, 3820 - 3831
http://www.nature.com/emboj/journal/v28/n24/abs/emboj2009365a.html

**Pretaporter, a *Drosophila* protein serving as a ligand for Draper in the phagocytosis of apoptotic cells**

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Phagocytic removal of cells undergoing apoptosis is necessary for animal development and tissue homeostasis. Draper, a homologue of the *Caenorhabditis elegans* phagocytosis receptor CED-1, is responsible for the phagocytosis of apoptotic cells in *Drosophila*, but its ligand presumably present on apoptotic cells remains unknown. An endoplasmic reticulum protein that binds to the extracellular region of Draper was isolated. Loss of this protein, which we name Pretaporter, led to a reduced level of apoptotic cell clearance in embryos, and the overexpression of *pretaporter* in the mutant flies rescued this defect. Results from genetic analyses suggested that Pretaporter functionally interacts with Draper and the corresponding signal mediators. Pretaporter was exposed at the cell surface after the induction of apoptosis, and cells artificially expressing Pretaporter at their surface became susceptible to Draper-mediated phagocytosis. Finally, the incubation with Pretaporter augmented the tyrosine-phosphorylation of Draper in phagocytic cells. These results collectively suggest that Pretaporter relocates from the endoplasmic reticulum to the cell surface during apoptosis to serve as a ligand for Draper in the phagocytosis of apoptotic cells.

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http://www.nature.com/emboj/journal/v28/n24/abs/emboj2009343a.html

**Spatial distribution of opsin-encoding mRNAs in the tiered larval retinas of the sunburst diving beetle *Thermonectus marmoratus* (Coleoptera: Dytiscidae)**

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Larvae of the sunburst diving beetle, *Thermonectus marmoratus*, have a cluster of six stemmata (E1-6) and one eye patch on each side of the head. Each eye has two retinas: a distal retina that is closer to the lens, and a proximal retina that lies directly underneath. The distal retinas of E1 and E2 are made of a dorsal and a ventral stack of at least twelve photoreceptor layers. Could this arrangement be used to compensate for lens chromatic aberration, with shorter wavelengths detected by the distal layers and longer wavelengths by the proximal layers? To answer this question we molecularly identified opsin genes and their expression patterns in these eyes. We found three opsin-encoding genes. The distal retinas of all six eyes express long-wavelength opsin (TmLW) mRNA, whereas the proximal retinas express ultraviolet opsin (TmUV I) mRNA. In the proximal retinas of E1 and E2, the TmUV I mRNA is expressed only in the dorsal stack. A second ultraviolet opsin mRNA (TmUV II), is expressed in the proximal retinas of E1 and E2 (both stacks). The finding that longer-wavelength opsins are expressed distally to shorter-wavelength opsins makes it unlikely that this retinal arrangement is used to compensate for lens chromatic aberration. In addition, we also described opsin expression patterns in the medial retina of E1 and in the non-tiered retina of the lensless eye patch. To our knowledge, this is also the first report of multiple UV opsins being expressed in the same stemma.

Journal of Experimental Biology 212, 3781-3794 (2009)
http://jeb.biologists.org/cgi/content/abstract/212/23/3781?etoc

**The *Drosophila* DHR96 nuclear receptor binds cholesterol and regulates cholesterol homeostasis**
Cholesterol homeostasis is required to maintain normal cellular function and avoid the deleterious effects of hypercholesterolemia. Here we show that the *Drosophila* DHR96 nuclear receptor binds cholesterol and is required for the coordinate transcriptional response of genes that are regulated by cholesterol and involved in cholesterol uptake, trafficking, and storage. *DHR96* mutants die when grown on low levels of cholesterol and accumulate excess cholesterol when maintained on a high-cholesterol diet. The cholesterol accumulation phenotype can be attributed to misregulation of *npc1b*, an ortholog of the mammalian Niemann-Pick C1-like 1 gene *NPC1L1*, which is essential for dietary cholesterol uptake. These studies define *DHR96* as a central regulator of cholesterol homeostasis.

Genes & Dev. 2009. 23: 2711-2716

http://genesdev.cshlp.org/content/23/23/2711.abstract

A novel histone fold domain-containing protein that replaces TAF6 in *Drosophila* SAGA is required for SAGA-dependent gene expression

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The histone acetyltransferase complex SAGA is well characterized as a coactivator complex in yeast. In this study of *Drosophila* SAGA (dSAGA), we describe three novel components that include an ortholog of Spt20, a potential ortholog of Sgf73/ATXN7, and a novel histone fold protein, SAF6 (SAGA factor-like TAF6). SAF6, which binds directly to TAF9, functions analogously in dSAGA to TAF6/TAF6L in the yeast and human SAGA complexes, respectively. Moreover, TAF6 in flies is restricted to TFIID. Mutations in saf6 disrupt SAGA-regulated gene expression without disrupting acetylated or ubiquitinated histone levels. Thus, SAF6 is essential for SAGA coactivator function independent of the enzymatic activities of the complex.

Genes & Dev. 2009. 23: 2818-2823

http://genesdev.cshlp.org/content/23/24/2818.abstract?etoc

Insect Neuroethology

Local and global motion preferences in descending neurons of the fly

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For a moving animal, optic flow is an important source of information about its ego-motion. In flies, the processing of optic flow is performed by motion sensitive tangential cells in the lobula plate. Amongst them, cells of the vertical system (VS cells) have receptive fields with similarities to optic flows generated during rotations around different body axes. Their output signals are further processed by pre-motor descending neurons. Here, we investigate the local motion preferences of two descending neurons called descending neurons of the ocellar and vertical system (DNOVS1 and DNOVS2). Using an LED arena subtending 240° × 95° of visual space, we mapped the receptive fields of DNOVS1 and DNOVS2 as well as those of their presynaptic elements, i.e. VS cells 1–10 and V2. The receptive field of DNOVS1 can be predicted in detail from the receptive fields of those VS cells that are most strongly coupled to the cell. The receptive field of DNOVS2 is a combination of V2 and VS cells receptive fields. Predicting the global motion preferences from the receptive field revealed a linear spatial integration in DNOVS1 and a superlinear spatial integration in DNOVS2. In addition, the superlinear integration of V2 output is necessary for DNOVS2 to differentiate between a roll rotation and a lift translation of the fly.

A descending contralateral directionally selective movement detector in the praying mantis *Tenodera aridifolia*

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Extracellular recordings were made from a directionally selective neuron in the ventral nerve cord of mantises. The neuron’s preferred direction of motion was forward and upward over the compound eye contralateral to its axon at the cervical connective. The neuron was sensitive to wide-field motion stimuli, resistant to habituation, and showed transient excitation in response to light ON and OFF stimuli. Its responses to drifting gratings depended on the temporal frequency and contrast of the stimulus. These results suggest that the neuron receives input from correlation-type motion detectors.

The target of rapamycin complex 2 controls dendritic tiling of *Drosophila* sensory neurons through the Tricornered kinase signalling pathway

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To cover the receptive field completely and non-redundantly, neurons of certain functional groups arrange tiling of their dendrites. In *Drosophila* class IV dendrite arborization (da) neurons, the NDR family kinase Tricornered (Trc) is required for homotypic repulsion of dendrites that facilitates dendritic tiling. We here report that Sin1, Rictor, and target of rapamycin (TOR), components of the TOR complex 2 (TORC2), are required for dendritic tiling of class IV da neurons. Similar to trc mutants, dendrites of sin1 and rictor mutants show inappropriate overlap of the dendritic fields. TORC2
components physically and genetically interact with Trc, consistent with a shared role in regulating dendritic tiling. Moreover, TORC2 is essential for Trc phosphorylation on a residue that is critical for Trc activity in vivo and in vitro. Remarkably, neuronal expression of a dominant active form of Trc rescues the tiling defects in sin1 and rictor mutants. These findings suggest that TORC2 likely acts together with the Trc signalling pathway to regulate the dendritic tiling of class IV da neurons, and thus uncover the first neuronal function of TORC2 in vivo.

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Imaging neural activity in worms, flies and mice with improved GCaMP calcium indicators

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Genetically encoded calcium indicators (GECIs) can be used to image activity in defined neuronal populations. However, current GECIs produce inferior signals compared to synthetic indicators and recording electrodes, precluding detection of low firing rates. We developed a single-wavelength GCaMP2-based GECI (GCaMP3), with increased baseline fluorescence (3-fold), increased dynamic range (3-fold) and higher affinity for calcium (1.3-fold). We detected GCaMP3 fluorescence changes triggered by single action potentials in pyramidal cell dendrites, with signal-to-noise ratio and photostability substantially better than those of GCaMP2, D3cpVenus and TN-XXL. In Caenorhabditis elegans chemosensory neurons and the Drosophila melanogaster antennal lobe, sensory stimulation–evoked fluorescence responses were significantly enhanced with GCaMP3 (4–6-fold). In somatosensory and motor cortical neurons in the intact mouse, GCaMP3 detected calcium transients with amplitudes linearly dependent on action potential number. Long-term imaging in the motor cortex of behaving mice revealed large fluorescence changes in imaged neurons over months.

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Leucine-rich repeat transmembrane proteins instruct discrete dendrite targeting in an olfactory map

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Olfactory systems utilize discrete neural pathways to process and integrate odorant information. In Drosophila, axons of first-order olfactory receptor neurons (ORNs) and dendrites of second-order projection neurons (PNs) form class-specific synaptic connections at ~50 glomeruli. The mechanisms underlying PN dendrite targeting to distinct glomeruli in a three-dimensional discrete neural map are unclear. We found that
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the leucine-rich repeat (LRR) transmembrane protein Capricious (Caps) was differentially expressed in different classes of PNs. Loss-of-function and gain-of-function studies indicated that Caps instructs the segregation of Caps-positive and Caps-negative PN dendrites to discrete glomerular targets. Moreover, Caps-mediated PN dendrite targeting was independent of presynaptic ORNs and did not involve homophilic interactions. The closely related protein Tartan was partially redundant with Caps. These LRR proteins are probably part of a combinatorial cell-surface code that instructs discrete olfactory map formation.

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Frequency Transitions in Odor-Evoked Neural Oscillations

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In many species, sensory stimuli elicit the oscillatory synchronization of groups of neurons. What determines the properties of these oscillations? In the olfactory system of the moth, we found that odors elicited oscillatory synchronization through a neural mechanism like that described in locust and Drosophila. During responses to long odor pulses, oscillations suddenly slowed as net olfactory receptor neuron (ORN) output decreased; thus, stimulus intensity appeared to determine oscillation frequency. However, changing the concentration of the odor had little effect upon oscillatory frequency. Our recordings in vivo and computational models based on these results suggested that the main effect of increasing odor concentration was to recruit additional, less well-tuned ORNs whose firing rates were tightly constrained by adaptation and saturation. Thus, in the periphery, concentration is encoded mainly by the size of the responsive ORN population, and oscillation frequency is set by the adaptation and saturation of this response.

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Glycogen synthase kinase-3/Shaggy mediates ethanol-induced excitotoxic cell death of Drosophila olfactory neurons

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It has long been known that heavy alcohol consumption leads to neuropathology and neuronal death. While the response of neurons to an ethanol insult is strongly influenced by genetic background, the underlying mechanisms are poorly understood. Here, we show that even a single intoxicating exposure to ethanol causes non-cell-autonomous apoptotic death specifically of Drosophila olfactory neurons, which is accompanied by a loss of a behavioral response to the smell of ethanol and a blackening of the third antennal segment. The Drosophila homolog of glycogen synthase kinase-3 (GSK-3)β, Shaggy, is required for ethanol-induced apoptosis. Consistent with this requirement, the GSK-3β inhibitor lithium protects against the neurotoxic effects of ethanol, indicating the possibility for pharmacological intervention in cases of alcohol-induced neurodegeneration. Ethanol-induced death of olfactory neurons requires both their neural activity and functional NMDA receptors. This system will allow the investigation of the
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genetic and molecular basis of ethanol-induced apoptosis in general and provide an understanding of the molecular role of GSK-3β in programmed cell death.

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Peripheral modulation of worker bee responses to queen mandibular pheromone

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It is generally accepted that young worker bees (Apis mellifera L.) are highly attracted to queen mandibular pheromone (QMP). Our results challenge this widely held view. We have found that unless young workers are exposed to QMP early in adult life, they, like foragers, avoid contact with this pheromone. Our data indicate that responses to QMP are regulated peripherally, at the level of the antennal sensory neurons, and that a window of opportunity exists in which QMP can alter a young bee's response to this critically important pheromone. Exposing young bees to QMP from the time of adult emergence reduces expression in the antennae of the D1-like dopamine receptor gene, Amdop1. Levels of Amdop3 transcript, on the other hand, and of the octopamine receptor gene Amoa1, are significantly higher in the antennae of bees strongly attracted to QMP than in bees showing no attraction to this pheromone. A decline in QMP attraction with age is accompanied by a fall in expression in worker antennae of the D2-like dopamine receptor, AmDOP3, a receptor that is selectively activated by QMP. Taken together, our findings suggest that QMP's actions peripherally not only suppress avoidance behavior, but also enhance attraction to QMP, thereby facilitating attendance of the queen.

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Insect Pharmacology

Transduction mechanism(s) of Na-saccharin in the blowfly Protophormia terraenovae: evidence for potassium and calcium conductance involvement

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The study on transduction mechanisms underlying bitter stimuli is a particularly intriguing challenge for taste researchers. The present study investigates, in the labellar chemosensilla of the blowfly Protophormia terraenovae, the transduction mechanism by which saccharin evokes the response of the “deterrent” cell, with particular attention to the contribution of K+ and Ca2+ current and the role of cyclic nucleotides, since second messengers modulate Ca2+, Cl− and K+ currents to different extents. As assessed by extracellular single-sensillum recordings, our results show that the addition of a Ca2+ chelator such as EGTA or the Ca2+ current blockers SK&F-96365, Mibebradil, Nifedipine and W-7 decrease the response of the “deterrent” cell to saccharin. A similar decreasing effect was also obtained following the addition of 4-aminopyridine, a K+ current blocker. On the contrary, the membrane-permeable cyclic nucleotide 8-bromoguanosine 3’,5’-cyclic monophosphate (8Br-cGMP) activates this cell and shows an additive effect when presented mixed with saccharin. Our results are consistent with the hypothesis that in the labellar chemosensilla of the blowfly both Ca2+ and K+ ions are involved in the transduction mechanism of the “deterrent” cell in response to saccharin. Our results also suggest a possible pathway common to saccharin and 8Br-cGMP.
Insect Photoreception

Specialized ommatidia of the polarization-sensitive dorsal rim area in the eye of monarch butterflies have non-functional reflecting tapeta

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Many insects exploit sky light polarization for navigation or cruising-course control. The detection of polarized sky light is mediated by the ommatidia of a small specialized part of the compound eye: the dorsal rim area (DRA). We describe the morphology and fine structure of the DRA in monarch butterflies (Danaus plexippus). The DRA consists of approximately 100 ommatidia forming a narrow ribbon along the dorsal eye margin. Each ommatidium contains two types of photoreceptor with mutually orthogonal microvilli orientations occurring in a 2:6 ratio. Within each rhabdomere, the microvilli are well aligned. Rhabdom structure and orientation remain constant at all retinal levels, but the rhabdom profiles, as seen in tangential sections through the DRA, change their orientations in a fan-like fashion from the frontal to the caudal end of the DRA. Whereas these properties (two microvillar orientations per rhabdom, microvillar alignment along rhabdomeres, ommatidial fan array) are typical for insect DRAs in general, we also report and discuss here a novel feature. The ommatidia of monarch butterflies are equipped with reflecting tapeta, which are directly connected to the proximal ends of the rhabdoms. Although tapeta are also present in the DRA, they are separated from the rhabdoms by a space of approximately 55 \( \mu \)m effectively inactivating them. This reduces self-screening effects, keeping polarization sensitivity of all photoreceptors of the DRA ommatidia both high and approximately equal.

Insect Physiology

Isoform- and cell-specific function of tyrosine decarboxylase in the Drosophila Malpighian tubule

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The biogenic amine tyramine (TA) is a potent diuretic factor when applied to the Malpighian tubule (MT) of Drosophila melanogaster, stimulating both urine production and transepithelial chloride conductance. Isolated MTs can respond not only to TA but also to its precursor, tyrosine; this observation led to the proposal that MTs are able to synthesize TA from applied tyrosine through the action of the enzyme tyrosine decarboxylase (TDC). In the current study it is shown that the non-neuronal isoform of TDC, Tdc1, is expressed in the principal cells of the MT. A mutant allele of Tdc1, Tdc1\(^{f03311}\), was identified that reduced expression of the mature Tdc1 transcript by greater than 100-fold. MTs isolated from Tdc1\(^{f03311}\) homozygous flies showed no significant depolarization of their transepithelial potential (TEP) or diuresis in response to tyrosine.
Insect Frontiers

Insect Sex Determination

The origin of a selfish B chromosome triggering paternal sex ratio in the parasitoid wasp *Trichogramma kaykai*

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This study uses molecular and cytogenetic methods to determine the origin of a B chromosome in some males of the wasp *Trichogramma kaykai*. This so-called paternal sex ratio (PSR) chromosome transmits only through sperm and shortly after fertilization triggers degeneration of the paternal genome, while keeping itself intact. The resulting embryos develop into haploid B-chromosome-carrying males. Another PSR chromosome with a very similar mode of action is found in the distantly related wasp *Nasonia vitripennis* and its origin was traced by transposon similarity to the genus *Trichomalopsis*, which is closely related to *Nasonia*. To determine whether both PSR chromosomes have a similar origin we aimed to reveal the origin of the *Trichogramma* PSR chromosome. Using fluorescent *in situ* hybridization, we discovered a major satellite repeat on the PSR chromosome, the 45S ribosomal DNA. Analysis of the internal transcribed spacer 2 (ITS2) of this repeat showed the presence of multiple ITS2 sequences on the PSR chromosome resembling either the ITS2 of *T. oleae* or of *T. kaykai*. We therefore conclude that the *Trichogramma* PSR chromosome originates from *T. oleae* or a *T. oleae*-like species. Our results are consistent with different origins for the PSR chromosomes in *Trichogramma* and *Nasonia*.

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Insect Society

Brood pheromone suppresses physiology of extreme longevity in honeybees (*Apis mellifera*)

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Honeybee (Apis mellifera) society is characterized by a helper caste of essentially sterile female bees called workers. Workers show striking changes in lifespan that correlate with changes in colony demography. When rearing sibling sisters (brood), workers survive for 3-6 weeks. When brood rearing declines, worker lifespan is 20 weeks or longer. Insects can survive unfavorable periods on endogenous stores of protein and lipid. The glycolipoprotein vitellogenin extends worker bee lifespan by functioning in free radical defense, immunity and behavioral control. Workers use vitellogenin in brood food synthesis, and the metabolic cost of brood rearing (nurse load) may consume vitellogenin stores and reduce worker longevity. Yet, in addition to consuming resources, brood secretes a primer pheromone that affects worker physiology and behavior. Odors and odor perception can influence invertebrate longevity but it is unknown whether brood pheromone modulates vitellogenin stores and survival. We address this question with a 2-factorial experiment where 12 colonies are exposed to combinations of absence vs presence of brood and brood pheromone. Over an age-course of 24 days, we monitor the amount of vitellogenin stored in workers’ fat body (adipose tissue). Thereafter, we track colony survival for 200 days. We demonstrate that brood rearing reduces worker vitellogenin stores and colony long-term survival. Yet also, we establish that the effects can result solely from exposure to brood pheromone. These findings indicate that molecular systems of extreme lifespan regulation are integrated with the sensory system of honeybees to respond to variation in a primer pheromone secreted from larvae.

http://jeb.biologists.org/cgi/content/abstract/212/23/3795?etoc

Flexible task allocation and the organization of work in ants

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Flexibility in task performance is essential for a robust system of division of labour. We investigated what factors determine which social insect workers respond to colony-level changes in task demand. We used radio-frequency identification technology to compare the roles of corpulence, age, spatial location and previous activity (intra-nest/extra-nest) in determining whether worker ants (Temnothorax albipennis) respond to an increase in demand for foraging or brood care. The less corpulent ants took on the extra foraging, irrespective of their age, previous activity or location in the nest, supporting a physiological threshold model. We found no relationship between ants that tended the extra brood and corpulence, age, spatial location or previous activity, but ants that transported the extra brood to the main brood pile were less corpulent and had high previous intra-nest activity. This supports spatial task-encounter and physiological threshold models for brood transport. Our data suggest a flexible task-allocation system allowing the colony to respond rapidly to changing needs, using a simple task-encounter system for generalized tasks, combined with physiologically based response thresholds for more specialized tasks. This could provide a social insect colony with a robust division of labour, flexibly allocating the workforce in response to current needs.

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Polymorphic social organization in an ant

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Identifying species exhibiting variation in social organization is an important step towards explaining the genetic and environmental factors underlying social evolution. In most studied populations of the ant *Leptothorax acervorum*, reproduction is shared among queens in multiple queen colonies (polygyny). By contrast, reports from other populations, but based on weaker evidence, suggest a single queen may monopolize all reproduction in multiple queen colonies (functional monogyny). Here we identify a marked polymorphism in social organization in this species, by conclusively showing that functional monogyny is exhibited in a Spanish population, showing that the social organization is stable and not purely a consequence of daughter queens overwintering, that daughter queen re-adoption is frequent and queen turnover is low. Importantly, we show that polygynous and functionally monogynous populations are not genetically distinct from one another based on mtDNA and nDNA. This suggests a recent evolutionary divergence between social phenotypes. Finally, when functionally monogynous and polygynous colonies were kept under identical laboratory conditions, social organization did not change, suggesting a genetic basis for the polymorphism. We discuss the implications of these findings to the study of reproductive skew.

http://rspb.royalsocietypublishing.org/content/276/1677/4423.abstract

Insect Vision

**Visual detection of diminutive floral guides in the bumblebee *Bombus terrestris* and in the honeybee *Apis mellifera***

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Many flowers display colour patterns comprising a large peripheral colour area that serves to attract flower visitors from some distance, and a small central, contrastingly coloured area made up by stamens or floral guides. In this study, we scaled down the size of floral guides to detect the minimal size bumblebees (*Bombus terrestris*) and honeybees (*Apis mellifera*) require for guidance. We analyzed the approach and the precise contact of the antennal tips with the floral guide of artificial flowers which precedes landing and inspection. Both bumblebees and honeybees were able to make antennal contact with circular floral guides which were 2 mm in diameter; bumblebees performed better than honeybees and antennated also at floral guides smaller than 2 mm. In discrimination experiments with bumblebees, a minimum floral guide size of 2 mm was required for discrimination between artificial flowers with and without floral guides. With increasing experience bumblebees targeted close to the site of reward instead of making antennal contact with the floral guide, whereas honeybees did not alter their initial behaviour with growing experience. Bumblebees and honeybees spontaneously target diminutive floral guides to achieve physical contact with flowers by means of their antennae which helps them to inspect flowers.

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Insect Review

**Are Bigger Brains Better?**

Lars Chittka¹ and Jeremy Niven²
Attempts to relate brain size to behaviour and cognition have rarely integrated information from insects with that from vertebrates. Many insects, however, demonstrate that highly differentiated motor repertoires, extensive social structures and cognition are possible with very small brains, emphasising that we need to understand the neural circuits, not just the size of brain regions, which underlie these feats. Neural network analyses show that cognitive features found in insects, such as numerosity, attention and categorisation-like processes, may require only very limited neuron numbers. Thus, brain size may have less of a relationship with behavioural repertoire and cognitive capacity than generally assumed, prompting the question of what large brains are for. Larger brains are, at least partly, a consequence of larger neurons that are necessary in large animals due to basic biophysical constraints. They also contain greater replication of neuronal circuits, adding precision to sensory processes, detail to perception, more parallel processing and enlarged storage capacity. Yet, these advantages are unlikely to produce the qualitative shifts in behaviour that are often assumed to accompany increased brain size. Instead, modularity and interconnectivity may be more important.
females and to subsequently determine if they are fit and receptive. Males can also use
the information they acquire in this process to change their courtship behavior and
reduce courtship of classes of targets that are inappropriate or unreceptive. In \textit{Drosophila},
courtship plasticity, in the form of both nonassociative and associative learning, has been
documented—the type of learning depending on the nature of the trainer. The conditions
in which the male is presented with the training target can profoundly alter the cues that
he finds salient and the longevity of the memory that he forms. With the exception of
habituation and sensitization, these types of plasticity have an operant component in that
the male must be courting to respond to the behavior-altering cues. Courtship plasticity
is therefore a complex and rich range of behaviors rather than a single entity. Our
understanding of these plastic behaviors has been enhanced by recent advances in our
understanding of the circuitry underlying courtship itself and the identification of
chemical cues that drive and modify the behavior. Courtship learning is providing a
window into how animals can use a variety of sensory inputs to modulate a decision
making process at many levels.

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\textbf{Circadian rhythms and the evolution of photoperiodic timing in insects}

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This review discusses possible evolutionary trends in insect photoperiodism, mainly from
a chronobiological perspective. A crucial step was the forging of a link between the
hormones regulating diapause and the systems of biological rhythms, circadian or
circannual, which have independently evolved in eukaryotes to synchronize physiology
and behaviour to the daily cycles of light and darkness. In many of these responses a
central feature is that the circadian system resets to a constant phase at the beginning of
the subjective night, and then 'measures' the duration of the next scotophase. In
'external coincidence', one version of such a clock, light now has a dual role. First, it
serves to entrain the circadian system to the stream of pulses making up the light/dark
cycle and, second, it regulates the nondiapause/diapause switch in development by
illuminating/not illuminating a specific light sensitive phase falling at the end of the
critical night length. Important work by A. D. Lees on the aphid \textit{Megoura viciae} using so-
called 'night interruption experiments' demonstrates that pulses falling early in the night
lead to long-day effects that are reversible by a subsequent dark period longer than the
critical night length and also show maximal sensitivity in the blue–green range of the
spectrum. Pulses falling in the latter half of the night, however, produce long-day effects
that are irreversible by a subsequent long-night and show a spectral sensitivity extending
into the red. With movement to higher latitudes, insects develop genetic clines in various
parameters, including critical night length, the number of long-night cycles needed for
diapause induction, the strength of the response, and the 'depth' or intensity of the
diapause thus induced. Evidence for these and other types of photoperiodic response
suggests that they provided strong selective advantages for insect survival.

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