much more stringent SAC response than the oocyte; the presence of even a single mis-aligned chromosome triggers a SAC arrest and leads to apoptosis, arguing that the dependence might be specific to the oocyte [20]. Importantly, the current study points to a possibility that cohesin might play a role in the difference in checkpoint stringency. Given the clinical importance of human aneuploidy, further elucidation of SAC regulation in the oocyte and understanding of male–female differences in the process are critical.

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Neuroethology: Lemon-Fresh Scent Makes Flies Lay Eggs

A new study reveals how *Drosophila* uses their sense of smell to decide on where to lay their eggs. These results have exciting implications for the evolution of fruit preference and parasitoid avoidance in fruit flies.

Jeffrey A. Riffell

> "When and where animals lay their eggs, a problem which has been studied under field conditions by many observers, demands analysis through experiment into terms of response to sensory stimuli. The process is more complicated than some other responses, and has been supposed to involve an element of foresight not usually attributed to many other activities."
>
> –Edward F. Adolph [1]

The ability to locate and decide on a suitable environment for offspring has important evolutionary and ecological implications for the next generation — the environment should nourish the young as well as protect them from predators. This is particularly important for insects, including flies, which tend to have larvae that cannot disperse far [2]. While a mechanistic understanding of the sensory stimuli and behaviors leading up to egg-laying has been lacking in the fruit fly (*Drosophila melanogaster*), egg deposition has been a valuable marker for determining adverse reactions to stimuli, host-plant preferences and identifying advantageous conditions for progeny development [3–5]. Despite the importance of the *Drosophila* as a model, and the genetic 'toolkit' allowing manipulation of the neural circuits controlling the behaviors, little is known about the neurons that underlie egg-laying behaviors. A fascinating new study in this issue of *Current Biology* [6] has taken an important step in identifying the neurophysiological bases of this behavior and the evolutionary implications for egg-laying preferences.

Many sensory cues have been shown to influence egg-laying behavior in fruit flies, including types of scent, color, taste and texture, to name just a few. For instance, temperature has shown to be an important cue for egg deposition [7], and flies prefer the color green [8]. Chemosensory cues are particularly important for egg-laying. The smell of acetic acid is a strong stimulant for egg-laying [9], and the presence of sugar has also shown to be important [10]. By contrast, emission of Geosmin from moldy fruit deters ovipositing females [11]. In the new study [6], Dweck, Stensmyr and colleagues identify the fruit volatiles emitted that flies prefer in their choice of egg-laying substrate. Although *D. melanogaster* is a generalist, they find that it exhibits marked preferences for *Citrus* fruits (Figure 1). In a series of multiple choice assays, flies were allowed to oviposit on different types of fruit and showed overwhelming preference for non-acidic *Citrus*.

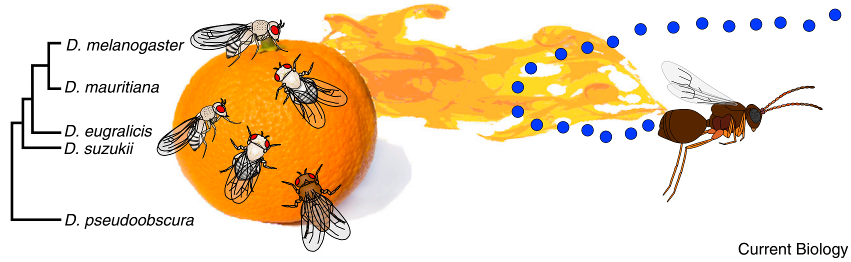

Figure 1. *Citrus* volatiles activate a conserved olfactory channel for stimulating oviposition in *Drosophila*.

Activation of the ai2A neurons and stimulating oviposition by the *Citrus* volatiles limonene and valencene is conserved across the subgenus *Sophophora* (*left*). The *Citrus* fruits — with their thick rinds — also act as a refuge for *Drosophila* larvae from parasitization. The emitted terpenes are aversive to a parasitoid wasp (*right*).

Scent, Neurophysiology and Behavior

How are egg-laying decisions being made, and what are the cues? Natural odors are complex bouquets composed of tens to hundreds of volatiles. Often these complex mixtures of compounds elicit behaviors different from the single volatiles. Yet, the attractive *Citrus* fruits all share a similar bouquet and volatiles (limonene, valencene) that are critical for egg-laying behavior. One of the attractive features of the study by Dweck *et al.* [6] is the demonstration that a single olfactory channel — via the olfactory receptor protein Or19a, expressed in the ai2A neuron on the antenna — is specific for limonene and valencene, and that silencing the ai2A neurons causes immediate deficits in behavior.

This raises the question regarding the role of different cues and modalities in controlling the egg-laying response. In flies, olfactory behaviors have been shown to be strongly regulated by taste and visual cues such that these sensory inputs ‘gate’ the olfactory behaviors. For example, male fly responses to the pheromone cVA are controlled by the tastant 7-tricosene, a non-volatile cuticular hydrocarbon [12]. Moreover, olfactory search behaviors can be modified by the presence of visual cues [13]. In the new study [6], Dweck *et al.* find that the *Citrus* volatiles limonene and valencene stimulate the egg-laying response, but do not attract the flies from a distance. This suggests that multiple cues are involved in the egg-laying decision. *Citrus* fruits emit a complex bouquet that is attractive to flies, and microbes that grow on fermenting fruits also emit attractive volatiles [14,15]. Thus, these volatiles might attract the flies from a distance, while limonene, in combination with fruit color, taste, and/or texture, might be the cue that flies use for deciding where to lay their eggs.

Beyond the work by Dweck *et al.* [6], there have been a few recent studies examining the neural basis of egg-laying behavior in *Drosophila* [9,10,16]. These studies have further shown the complex interplay between sensory modalities and cues. For example, when flies taste acetic acid on the fermenting fruit, egg-laying is strongly stimulated. However, smelling acetic acid causes them to avoid certain areas of the fruit [9]. Thus a single cue can activate different sensory modalities and cause different behaviors. These behavioral preferences provide an interesting system by which to examine the neural basis of egg-laying, and how different cues control such decision-making processes.

Scent, Neurophysiology and Evolution

The *Citrus–Drosophila* relationship presents an intriguing system to study the origin of olfactory preferences and effects of dispersal and gene flow in maintaining that preference. The African origin of *D. melanogaster* and the Asian origin of *Citrus* suggest several mechanisms for how the fly’s behavioral preference may have arisen: *Citrus* may activate a preexisting olfactory bias or, alternatively, the preference may be an ancestral trait from an Asian population colonizing Africa. Indeed, when Dweck *et al.* [6] examined the responses of the ai2A neuron to *Citrus* volatiles in a variety of *Drosophila* species — both distantly related and closely related to *D. melanogaster* — they found that the Asian relatives exhibited responses similar to *D. melanogaster.* This is a fascinating result given the rapid evolution of olfactory receptor proteins and host responses [17,18]. Furthermore, these results raise the question: what selective forces might maintain the tuning of the ai2A neuron and the behavioral preferences of the *Drosophila* species to limonene?

Parasitization and predation can exert strong selective pressures on egg-laying decisions. For instance, mosquitoes can sense the presence of predators in pools, and thus only oviposit in pools that lack predators [19]. For *Drosophila* larvae, parasitization by wasps is a major source of mortality. *Citrus* fruits, with their tough rinds, may offer a physical barrier and refugia for larvae against parasitoid wasps, thus causing them to be highly preferred by gravid female flies. Furthermore, the ability to smell and avoid the *Citrus* fruits may be beneficial for the wasp, if the attempt to locate the larvae through the rind is costly in time and energy. Indeed, when Dweck *et al.* [6] tested the preferences of a parasitic wasp (*Leptopilina boulardi*) that specializes on *Drosophila* larvae, they found that olfactory neurons on the wasp antennae were highly responsive to *Citrus* volatiles, such as limonene and valencene, and that these volatiles were avoided by searching wasps (Figure 1). Thus, the same cue that indicates host suitability for flies also indicates host unsuitability for parasitoids.

Regardless of the selective pressures on the ai2A neuron, or the evolutionary basis of the fly–*Citrus* relationship, it is clear that limonene and valencene are potent activators of the ai2A neuron. Furthermore, this study brings up several questions for future research: for instance, how do responses of the Or19a receptor and the ai2A neurons compare between the different *Drosophila* species, especially those that are specialized for specific hosts (e.g., *D. mojavensis*)? At the level of the fly antennal lobe, the primary processing center of olfactory information, how does the DC1 glomerulus, which receives input from the ai2A neurons, process this information when other host odors are applied, and does the antennal lobe representation change with the different stimuli? How does this relate to behavior? Finally, *D. melanogaster* is a human commensal with a cosmopolitan distribution owing to human activities. Although *D. melanogaster* originated in Africa, its exact native environment remains unknown. Thus, discovery of African fruits that emit limonene and valencene could open the possibility of identifying the habitats where *D. melanogaster* originated as a means to learn the fly's natural history before it became associated with humans.

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Visual Attention: A Rhythmic Process?

Vision involves constant exploration of the environment by eye movements. Recent evidence suggests that a rhythmic form of exploration also occurs under covert attention, in the absence of eye movements. Sustained attention naturally fluctuates, with a periodicity in the theta (4–8 Hz) frequency range.

Rufin VanRullen[1,2]

Even when the visual scene is entirely static, visual perception is dynamically reestablished with every eye blink, saccade and micro-saccade. This is one way for the brain to optimize the so-called 'exploitation/exploration' trade-off: collecting reliable information from each eye fixation while simultaneously monitoring all potentially relevant parts of the world. Covert visual attention is sometimes viewed as an evolutionary shortcut allowing the brain to preferentially process selected locations without the energetic costs associated with eye movements [1]. As such, covert attention faces the same exploitation/exploration problem. Recent evidence, including a study by Fiebelkorn *et al.* [2] in this issue of *Current Biology*, suggests that this problem is tackled by a 7–8 Hz rhythmic sampling strategy akin to ocular exploration; even when attention concentrates on a single target, its samples are periodically interrupted, as if attention 'blinked' regularly [3], just like the eyes do.

In the new study by Fiebelkorn *et al.* [2], participants monitored a display made up of two rectangular objects in order to detect a brief target (Figure 1A). At the beginning of each display, a cue served to anchor attention at the end of one of the objects. Detection performance was measured at various times following the cue (10 ms resolution) to reveal the temporal behavior of attention at three possible locations: the cue location, the opposite end of the cued object (same-object location), and the nearest end of the other object (different-object location). As expected from classic attention studies, raw detection performance curves were highest at the cued location (due to spatial attention), and also increased at the same-object location compared to the different-object location (due to 'object-based' attention), even though these two locations were equidistant from the cue. Surprisingly, however, all three curves also displayed significant temporal performance fluctuations (Figure 1B). More precisely, performance at the cue