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.

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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

location and same-object location oscillated at both 7–8 Hz and ~4 Hz (though this latter oscillation did not reach significance for the cue location), while performance at the different-object location oscillated selectively at ~4 Hz. This confirms that attention is not a static process, but an intrinsically rhythmic one.

Next, Fiebelkorn *et al.* [2] investigated the phase relationships between locations that fluctuated in the same frequency range. At 7–8 Hz, the cue location was sampled first in each cycle, followed by the same-object location after approximately 1/4 cycle (or ~30 ms). In other words, attention seemed to sweep periodically across the object. At ~4 Hz, the same-object and different-object locations were sampled in an anti-phase pattern, i.e. about 125 ms apart (the corresponding phase relations with cue location were not reported since the ~4 Hz oscillation was not significant at the cue location). One possibility is that this anti-phase sampling at ~4 Hz actually reflects alternating samples taken from each object at the original 7–8 Hz rate. This would imply that a unique attentional rhythm at 7–8 Hz could sometimes sample the target object by sweeping across it periodically ('within-object sampling' in Figure 1), and sometimes distribute its resources across multiple objects (cued or uncued) by sampling them sequentially ('between-object sampling' in Figure 1). Because the temporal fluctuations were not directly measured on each trial, but only indirectly estimated by averaging single-time-point measurements across independent trials, it is not possible to determine whether these two modes of sampling (within- and between-object) occurred simultaneously, or at different moments in time or even on different trials.

Other recent studies have foreshadowed the present findings (reviewed in [4]). Perhaps the earliest explicit demonstration of a 7–8 Hz attentional rhythmicity was published by our team in 2007 [3]. We measured human psychometric functions for target detection as a function of target duration at various set sizes (the number of possible targets). Upon fitting different models of attention deployment to the human data, we concluded that an ongoing rhythmic attention process serially sampled the targets at a rate of ~7 per second; furthermore, this rhythmic sampling
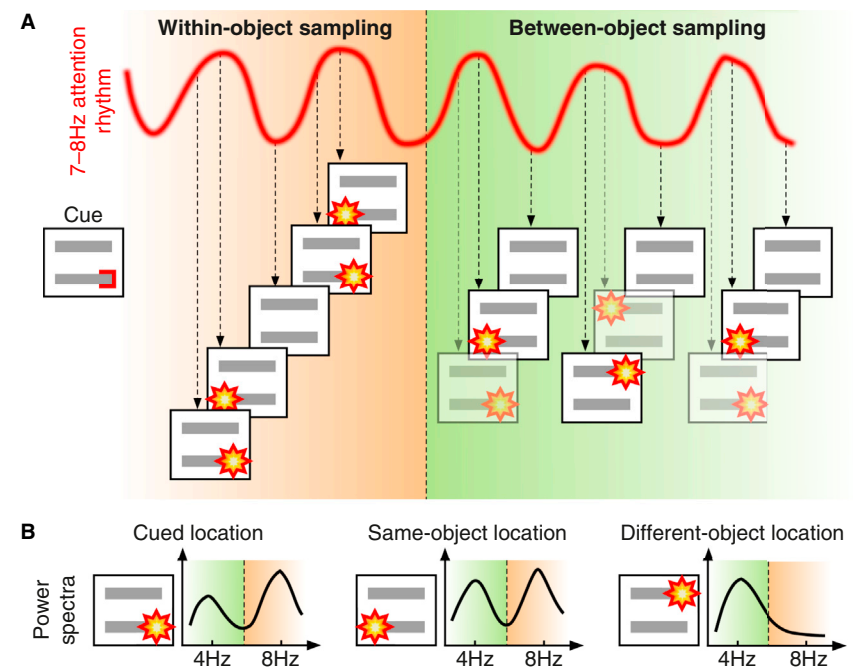
Figure 1. Rhythmic attentional sampling within and between objects.

(A) Following a cue event on one side of an object, spatial attention (illustrated by the 'star' symbol) is periodically deployed to this location at 7–8 Hz. It also samples the other side of the same object on each cycle (object-based attention), but with a slight phase delay, as if attention was sweeping across the object. Rhythmic fluctuations in performance can also be measured on the other, uncued object, albeit at a lower frequency of ~4 Hz; in this case, they alternate (in phase opposition) with periods of enhanced processing of the cued object. In other words, successive attentional cycles at 7–8 Hz appear to sample alternate objects. (The dimmed displays indicate conditions that either did not reach statistical significance or were not tested in the experiment by Fiebelkorn *et al*. [2].) These two modes of attention (within- and between-object sampling) may take place simultaneously, under the influence of independent perceptual mechanisms. But they could also be produced by a single rhythmic attentional process, which in different trials or at different moments would sample one or multiple objects. (B) Power spectra of performance fluctuations for each of the three tested locations. Both the cued location and the other location of the same object (but not the uncued object) show fluctuations at 7–8 Hz reflecting within-object sampling. All three locations also display fluctuations at half this rate (~4 Hz) due to between-object sampling.

persisted even when attention was sustained towards a single target location (as in Figure 1). Subsequently, we used electroencephalography (EEG) to uncover the electrophysiological correlates of this ongoing attentional sampling [5]: we showed that the detection of a threshold peripheral flash depended on the precise phase of ~7 Hz EEG oscillations just before flash onset — but only when the flash location was attended. This result suggests that ~7 Hz ongoing brain oscillations can reflect rapid fluctuations of attention, with each ~7 Hz cycle indexing a separate attention sample.

In these earlier studies we strained to access an ongoing attentional sampling rhythm that we assumed

would be strictly spontaneous, and thus would have different — and a *priori* unknown — timing on every trial. However, as more recent studies have now shown [2,6,7], the sampling rhythm can actually be reset by an appropriate spatio-temporal cue; this makes it a good deal more practical to investigate attentional fluctuations, by directly measuring behavioral performance (with high temporal resolution) at various moments after the cue. For example, Landau and Fries [6] showed that a brief cue delivered around one of two simultaneously monitored targets would reset an attentional sampling mechanism that became visible as an anti-phase pattern of ~4 Hz performance fluctuations for each target location. This corresponds to the

between-object sampling situation illustrated in Figure 1. The new study by Fiebelkorn *et al.* [2] improved on this paradigm to address the question of object-based attention, allowing them to reveal within a single dataset both the periodic nature of attention (within-object sampling) and its sequential exploratory behavior (between-object sampling). Only one of our above-mentioned studies had achieved this before, via the modeling of psychometric functions [3].

How can the exploratory (between-object) sampling of attention operate when there are more than two objects in a scene? If 7–8 samples are taken every second but from each object in alternation, one should predict that the effective sampling rate at each location decreases when the set size increases. This prediction was directly verified in two recent studies, one using multiple-object tracking [8] and the other using the continuous wagon-wheel illusion [9] to measure the temporal resolution of attention. In both cases, the estimated sampling rate of attention decreased more than twofold between a single-target situation and one with three [8] or four [9] simultaneous targets.

Is this emerging notion of rhythmic sampling compatible with standard views on attention? Many classic theories of attention (such as the feature-integration [10] or the saliency map [11] theories) assume a unique, indivisible 'spotlight' that must dynamically shift around to explore different objects in a scene. Yet few of them predicted that this exploration would occur rhythmically, especially not in single-target situations (within-object sampling). Notably, however, both the selective tuning model [12] and the communication-through-coherence theory [13] have explicitly proposed

that attentional selection may be broken and periodically reinstated every 150–200 ms.

This figure, 150–200 ms per attention sample, falls within the theta-frequency range, and is consistent with classic psychophysical estimates of attention dwell time [14,15]. But it is an order of magnitude too slow to directly explain serial search slopes, a typical reaction time increase of 20–50 ms/item in complex visual search arrays [10,16]. One recent study using monkey neuronal recordings [17] did report evidence for serial sampling of search elements at a rate of 18–34 Hz, more directly compatible with search slopes of ~30–50 ms/item. Yet another (non-exclusive) explanation could be that each slower 7–8 Hz attention sample encompasses multiple items during visual search, thus increasing the effective sampling rate of attention.

In conclusion, evidence that covert attention involves 7–8 Hz rhythmic sampling is piling up. The new study by Fiebelkorn *et al.* [2] confirms this notion, and shows that the sampling is not restricted to an explicitly cued location but also spreads to other parts of the same object, and can occasionally even explore other objects. A particularly promising new finding is the robust phase offset between locations from the same object. Do the cycles of attention actually scan the world like a propagating wave? The rhythms of attention may still have more secrets to reveal.

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