the deceptive spots in the non-deceptive morphotypes, either through introgression by serial backcrossing, or through direct transgenic manipulations? Further, is there a regulatory hierarchy between these three modules, or is the composite phenotype the result of phenotypic integration? Lastly, what determines the spatial patterning of the spots within an individual floret, and could this within-floret patterning be due to additional co-option events? Truly, *G. diffusa* is a seductive emerging model system for the study of composite phenotypic novelty.

And just in case anyone is still left worrying about the hapless bee fly, fear not. Male bee flies do learn to recognize the patterns associated with sexually deceptive morphotypes and will avoid them for at least a short time after the encounter[16].

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Active vision: How you look reflects what you are looking for

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While we fixate an object, our eyes are never stationary but constantly drifting, with miniature movements traditionally thought to be random and involuntary. A new study shows that the orientation of such drift in humans is actually not random but is influenced by the task demands to improve performance.

Traditionally, visual perception in humans has been conceptualized and studied as involving two processing phases that are relatively independent of each other: an 'exploratory' phase, where the eyes move around the environment searching for objects of interest on which to focus, and an 'exploitative' phase, where sensory information is acquired during stable fixation. In recent years, numerous lines of evidence have challenged this dichotomy, reframing vision as an active process that involves a constant interplay between perception and action[1]. For instance, even during periods of fixation, the eye is
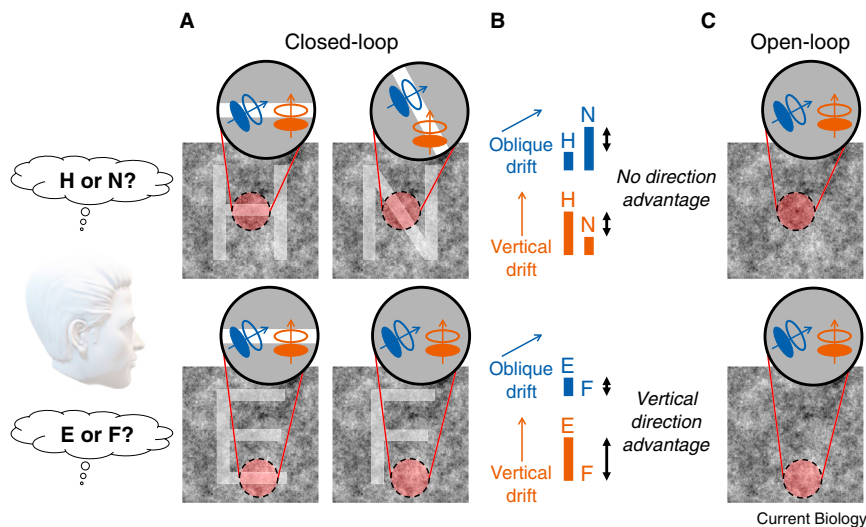
Figure 1. Letter discrimination task and schematic neuronal responses as a function of ocular drift direction.
(A) In different blocks, subjects were asked to discriminate between pairs of very small (1.5 degrees of visual angle) letters superimposed on a noisy background (H or N in HN blocks, E or F in EF blocks). The letters in the HN pair vary in the orientation of the central stroke, the letters in the EF pair vary in the presence/absence of a bottom horizontal stroke. The schematic receptive fields of two orientation-selective 'simple-like cells' in the primary visual cortex are shown in blue and orange for cells selective for oblique or horizontal edges, respectively. Cells in the primary visual cortex (or even a standard retinal ganglion cell model) fire more in response to stimuli moving orthogonally to their preferred orientation. (B) Vertical bars show the firing rates of such cells during oblique (blue) and vertical (orange) ocular drift, for each letter. Both oblique and vertical drift provide an equal amplitude difference signal for discriminating between an N and an H (equal black double-headed arrows), but a vertical drift is more beneficial for discriminating an E from an F (a larger double-headed black arrow). Indeed, subjects showed more vertical drift in EF blocks as compared to HN blocks. (C) In the open-loop trials where letters were absent, a prolonged search for a letter resulted in an even larger amount of the vertical drift in EF blocks.

never stationary, but continuously engaged in a seemingly erratic motion, known as ocular drift. Earlier work has shown that, although ocular drift has traditionally been thought to be a random and involuntary movement, it is influenced by the nature of the visual target[2,3], and further, that the visual system has access to high-resolution extraretinal information about fixational eye movements and uses it to infer spatial relationships[4]. Indeed, in a recent *Current Biology* dispatch[5] on the importance of the saccade–drift cycle in reformatting spatiotemporal visual inputs, we pondered whether, similarly to the smallest microsaccades that can be accurately directed to the most sensitive part of fovea, ocular drift might also be precisely controlled and adapted to the current requirements[6]. In an intriguing study reported in this issue of *Current Biology*, Lin *et al.*[7] directly tested the very nature of the detailed visuomotor interaction during fixation, providing a positive answer to this question.

The work of Lin *et al.*[7] was based on two known facts about the primate visual

system: that ocular drift causes a continuous retinal motion; and that neurons in the primary visual cortex prefer stimuli moving orthogonal to their preferred orientation. On this basis, the authors posed a simple question: does drift orientation in human observers adapt to the characteristics of the stimulus to enhance its processing? To answer this question, they selected two pairs of letters to be discriminated: E *versus* F, and H *versus* N. Figure 1 shows why vertical retinal motion is more effective (in terms of neural coding) for distinguishing between an E and an F, whereas it is no better than oblique motion in differentiating between an H and an N. One would expect the drift to be accentuated in the direction orthogonal to the spatial frequency components that distinguish between the letters. Hence, the ratio of vertical drifts to oblique drifts is expected to be greater when observers try to discriminate E *versus* F, than for H *versus* N discrimination. Following this prediction, the authors developed a simple, although technically challenging, and clever

experiment: in certain blocks (EF trials), participants were shown an E or an F letter; in other blocks (HN trials), they were shown an H or an N letter. Eye movements were recorded with great precision and accuracy, and authors examined how the orientation of ocular drift differed between conditions. Crucially, the letters to differentiate within each block were known to the participants in advance, and 20% of trials (unbeknownst to participants) contained no letter but only visual noise.

Lin *et al.*[7] compared the amount of vertical and oblique drift motion for the EF and HN trials. In line with the above-mentioned hypothesis, vertical motion was found to be more prominent for EF than HN trials, indicating that ocular drift orientation could be adapted to improve task performance. The authors next asked whether the visual activation is needed to bias the drift direction, or whether the bias is emerging from purely perceptual expectation due to task knowledge. In other words, is this modulation due to visual feedback (closed-loop), or is it driven by task knowledge (open-loop)? Perhaps surprisingly at first glance, the effect was even more prominent in trials where the letter was not shown. The finding that participants' knowledge of the task influenced ocular drift orientation even in the absence of any visual feedback suggests that this effect is primarily driven by open-loop control mechanisms. A stronger bias in the open-loop condition might be due to a longer search phase when no letters are present, and no stimulus is 'anchoring' the drift, allowing for the cognitive influence to transpire more fully.

Arguably even more so than drifts, fixational saccades or microsaccades, small ballistic eye movements that occur during attempted fixation, are also influenced and precisely controlled by cognitive factors[5]. Microsaccades are known to counteract gaze offsets introduced by the ocular drift[8–10]. Lin *et al.*[7] found that the landing points of microsaccades were different in HN *versus* EF trials, which raises the important question of whether the effect observed in the drift could be explained by differences in microsaccades. Crucially, the orientation bias held also when considering trials without microsaccades, indicating that the effect genuinely reflected processes related to

ocular drift. Notably, this result seems to suggest the presence of a functional and physiological dissociation in how ocular drift and microsaccades are generated and controlled during vision. To date, however, the neural mechanisms for controlling ocular drift are still largely unknown, and this fundamental aspect is certainly worthy of further investigations.

Ocular drift dynamics have been associated with visual acuity thresholds both within and across observers[3,11]. However, there is still debate over the direction of causality: are variations in drift dynamics caused by differences in visual acuity or, instead, are variations in drift the cause of these differences? This is a crucial question, one that the new Lin et al.[7] study might help to clarify. Indeed, in an attempt to resolve the visual stimulus when letters were omitted, participants tended to maximize the amount of motion orthogonal to the feature that distinguished the expected letters. These dynamics were not driven by visual feedback, as no stimulus was presented. Instead, by virtue of the characteristics of the visual neurons, it likely caused a change in response gain for those visual channels involved in the discrimination task, possibly resulting in enhanced visual acuity. Therefore, the presence of a prominent 'open-loop' process in the current study seems to indicate that eye movement dynamics can shape visual responses. This is well in line with dynamic theories of visual acuity[12,13] and with predictions based on modelling retinal ganglion cell responses in the presence of fixational eye movements[14,15]. Open-loop effects do not imply, however, that visual responses cannot modulate the dynamics of the drift; indeed, based on his pioneering work, Steinman[16] argued long ago that the drift, which he called 'slow control', is based on the stimulus[6]. The two hypotheses, much like in the chicken-or-egg dilemma, are not mutually exclusive: stimulus expectation influences drift, the drift influences visual responses, which in turn influence the drift. But the role of visual feedback seems to be marginal at least in the context of the Lin et al.[7] study.

More generally, the Lin et al.[7] study opens a window onto an important dispute among researchers in the field of eye movements. Does the fact that ocular drift is under cognitive influence imply that it should be considered a goal-directed or even a voluntary movement, similar to larger saccades? The debate over the 'voluntariness' of a movement largely comes down to problems of language and/or definition and is sometimes entangled in issues related to conscious awareness and free will that are well beyond the scope of this dispatch. Here, what we would like to emphasize most is that even at this miniature spatial scale, the eye movements are not random. Although the drift largely follows a random-like fluctuation — whose statistical characteristics might be important for increasing the computational efficiency of vision[17] — its orientation is clearly influenced by contextual factors and the subject's expectations. In these terms, the observable bias in drift orientation is, in some sense, voluntary in that it is an expectation-driven movement. It is undoubtedly a very interesting question for future work whether people are (or can be made) consciously aware of these biases.

Finally, a plethora of neurological disorders — including macular degeneration, Alzheimer's disease, and mild cognitive impairment — are known to cause alterations in the dynamics of fixational eye movements[18–20]. The evidence that cognitive factors can influence ocular drift orientation might therefore provide a new and promising framework for studying, understanding, and possibly screening these disorders. Moreover, the fact the visual system can exploit the drift orientation to improve vision, particularly high acuity vision, might also help in developing and testing new tools, such as *text fonts*, to alleviate visual disabilities, including dyslexia and low vision.

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