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Theory of morphodynamic information processing: Linking sensing to behaviour

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ABSTRACT

The traditional understanding of brain function has predominantly focused on chemical and electrical processes. However, new research in fruit fly (*Drosophila*) binocular vision reveals ultrafast photomechanical photoreceptor movements significantly enhance information processing, thereby impacting a fly's perception of its environment and behaviour. The coding advantages resulting from these mechanical processes suggest that similar physical motion-based coding strategies may affect neural communication ubiquitously. The theory of neural morphodynamics proposes that rapid biomechanical movements and microstructural changes at the level of neurons and synapses enhance the speed and efficiency of sensory information processing, intrinsic thoughts, and actions by regulating neural information in a phasic manner. We propose that morphodynamic information processing evolved to drive predictive coding, synchronising cognitive processes across neural networks to match the behavioural demands at hand effectively.

1. Introduction

Behaviour arises from intrinsic changes in brain activity and responses to external stimuli, guided by animals' heritable characteristics and cognition that shape and adjust nervous systems to maximise survival. In this dynamic world governed by the laws of thermodynamics, brains are never static. Instead, their inner workings actively utilise and store electrochemical, kinetic, and thermal energy, constantly moving and adapting in response to intrinsic activity and environmental shifts orchestrated by genetic information encoded in DNA. However, our attempts to comprehend the resulting neural information sampling, processing, and codes often rely on stationarity assumptions and reductionist behaviour or reductionist brain activity analyses. Unfortunately, these preconceptions can prevent us from appreciating the role of rapid biomechanical movements and microstructural changes of neurons and synapses, which we call neural morphodynamics, in sensing and behaviours.

While electron-microscopic brain atlases provide detailed wiring maps at the level of individual synapses (Eichler et al., 2017; Meinertzhagen and O'Neil, 1991; Oh et al., 2014; Rivera-Alba et al., 2011; Winding et al., 2023), they fail to capture the continuous motion of cells. Fully developed neurons actively move, with their constituent molecules, molecular structures, dendritic spines and cell bodies engaging in twitching motions that facilitate signal processing and plasticity (Bocchero et al., 2020; Crick, 1982; Hardie and Franze, 2012; Hudspeth, 2008; Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022; Korkotian and Segal, 2001; Majewska and Sur, 2003; Pandiyan et al., 2020; Reshetniak and Rizzoli, 2021; Reshetniak et al., 2020; Rusakov et al., 2011; Senthilan et al., 2012) (Fig. 1**A-E**). Additionally, high-speed in vivo X-ray holography (Kemppainen et al., 2022), electrophysiology (Juusola et al., 1995) and calcium-imaging (Majewska and Sur, 2003) of neural activity suggest that ultrafast bursty or microsaccadic motion influences the release of neurotransmitter quanta, adding an extra layer of complexity to neuronal processing.

Recent findings on sensory organs and graded potential synapses provide compelling evidence for the crucial role of rapid morphodynamic changes in neural information sampling and synaptic communication (Bocchero et al., 2020; Juusola et al., 1995; Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022; Pandiyan et al., 2020; Schoneich and Hedwig, 2010; Watanabe et al., 2013). In *Drosophila*, these phasic changes enhance performance and efficiency by synchronising responses to moving stimuli, effectively operating as a

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form of predictive coding (Juusola et al., 2017; Kemppainen et al., 2022). These changes empower the small fly brain to achieve remarkable capabilities (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022), such as hyperacute stereovision (Kemppainen et al., 2022) and time-normalised and aliasing-free responsiveness to naturalistic light contrasts of changing velocity, starting from photoreceptors and the first visual synapse (Juusola et al., 2017; Zheng et al., 2009). Importantly, given the compound eyes' small size, these encoding tasks would only be physically possible with active movements (Juusola et al., 2017; Kemppainen et al., 2022; Zheng et al., 2009). Ultrafast photoreceptor microsaccades enable flies to perceive 2- and 3-dimensional patterns 4–10 times finer than the static pixelation limit imposed by photoreceptor spacing (Barlow and Rosenblith, 1961; Darwin, 1859), as demonstrated by behavioural experiments. Calcium imaging further supports this by showing that visual interneurons in both the lamina (L2) (Kemppainen et al., 2022) and lobula (LC18) (Klapoetke et al., 2022) optic lobes detect hyperacute (≤1°) bars, significantly finer than the ~ 4-7° acuity predicted by static optics at different locations in the

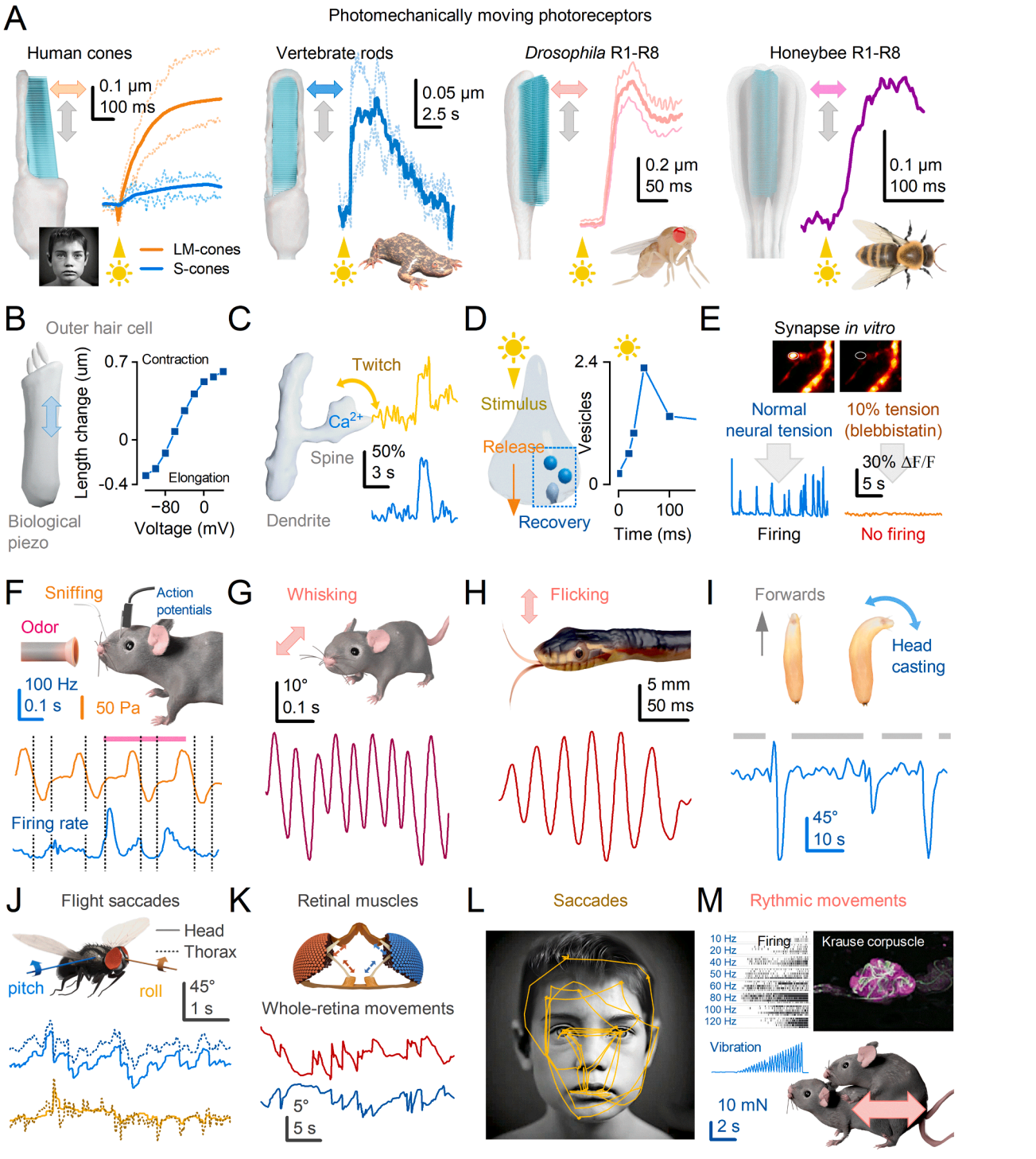

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Fig. 1. Sensory cells and central neurons, along with their morphodynamic components, dynamically respond to changes in information flow through phasic mechanical movements (A-E), exerting influence on sensory perception and behaviour (E-M). (A) Both vertebrate (Bocchero et al., 2020; Pandiyan et al., 2020) (human cones; rods in clawed frogs) and invertebrate (open-rhabdoms in fruit flies; fused apposition-type in rhabdoms in honeybee) photoreceptors (Bocchero et al., 2020; Hardie and Franze, 2012; Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022) exhibit ultrafast photomechanical movements in response to changes in light intensity. (B) Outer hair cells (Fettiplace et al., 2006; Kennedy et al., 2005) contract and elongate, amplifying variations in soundwave signals (Hudspeth, 2008). (C) Dendritic spines undergo twitching (Korkotian and Segal, 2001; Majewska and Sur, 2003) motions while sampling synaptic information. (D) Synapses undergo ultrafast structural changes and tissue movements, actively participating in and optimising information transmission (Juusola et al., 1995; Juusola et al., 1996; Majewska and Sur, 2003; Reshetniak and Rizzoli, 2021; Reshetniak et al., 2020; Rusakov et al., 2011; Watanabe et al., 2013; Zheng et al., 2006). (E) Synaptic transmission depends on tissue contractility (Joy et al., 2023). Treatment with blebbistatin inhibits this contractility, effectively silencing synapses (Joy et al., 2023). (F) Rats and humans employ quick sniffs to enhance odour detection (Shusterman et al., 2011; Smear et al., 2011). (G) Rodents' fast whisking motion enhances the perception of environmental structure (Bush et al., 2016). (H) Snakes flick their tongues to localise the source of odours better (Daghfous et al., 2012). (I) Larvae perform rapid head casting to determine the direction towards higher food concentration (Davies et al., 2015; Gomez-Marin et al., 2011). (J) Flies utilise fast saccadic eye and body movements to observe the world (Land, 2019; van Hateren and Schilstra, 1999). (K) During goal-oriented behaviours, flies use intraocular muscle-induced whole-retina movements (mini-arrows) that are larger than photoreceptor microsaccades (A), as observed in binocular vergence (left retina: red; right retina: blue), to enhance perception(Fenk et al., 2022; Franceschini and Taddei-Ferretti, 1998; Franceschini et al., 1995). (L) Humans (Schutz et al., 2011) perceive the world through saccadic eye movements(Land, 2019), where microsaccadic jitter (eyeball tremor) enhances the temporal coding of the visual space (Casile et al., 2019; Rucci et al., 2007) and improves the discrimination of high-frequency visual patterns (Intoy et al., 2024; Rucci and Victor, 2015). (M) Rhythmic sexual movements, such as those of mice, activate frequency-specific Krause corpuscles (tuned to dynamic, light touch and mechanical vibration) in the genitalia (Qi et al., 2024), enhancing tactile sensing and pleasure. Note that the human face in (A) and (L) is AI-generated and not real. Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

compound eye (Gonzalez-Bellido et al., 2011). Thus, neural morphodynamics can be considered a natural extension of animals' efficient saccadic encoding strategy to maximise sensory information while linking perception with behaviour (Fig. 1**F-M**) (Bush et al., 2016; Daghfous et al., 2012; Davies et al., 2015; Juusola et al., 2017; Kemppainen et al., 2022; Smear et al., 2011; van Hateren and Schilstra, 1999).

Overarching questions remain: Are morphodynamic information sampling and processing prevalent across all brain networks, coevolving with morphodynamic sensing to amplify environmental perception, action planning, and behavioural execution? How does the genetic information, accumulated over hundreds of millions of years and stored in DNA, shape and drive brain morphodynamics to maximise the sampling and utilisation of sensory information within the biological neural networks of animals throughout their relatively short lifespans, ultimately improving fitness? Despite the diverse functions and morphologies observed in animals, operating similar molecular motors and reaction cascades within compartmentalised substructures by their neurons suggests that the morphodynamic code may be universal.

This review delves into this phenomenon, specifically focusing on recent discoveries in insect vision and visually guided behaviour. Insects have adapted to colonise all habitats except the deep sea, producing complex building behaviour and societies, exemplified by ants, bees, and termites. Furthermore, insects possess remarkable cognitive abilities that often rely on hyperacute perception. For instance, paper wasps can recognise individual faces among their peers (Miller et al., 2020; Sheehan and Tibbetts, 2011), while *Drosophila* can distinguish minute parasitic wasp females from harmless males (Kacsoh et al., 2013). Hyperacute coloured patterns of flat images depicting copulating *Drosophila* can also trigger mate-copying behaviour in virgin, naïve observer females, even in the absence of olfactory or other sensory cues (Nöbel et al., 2022). These findings challenge the prevailing theoretical concepts (Land, 1997; Laughlin, 1989) that insects perceive a "pixelated," low-resolution image of the world, constrained by the ommatidial faceting that sets photoreceptor spacing. From the experimental positions, the tested visual patterns would occupy only a pixel or two at most, making the reliable detection of small, low-contrast feature differences physically impossible for static, low-resolution compound eyes, as demonstrated by modelling (Juusola et al., 2017; Kemppainen et al., 2022). Instead, we elucidate how such heightened performance naturally emerges from ultrafast morphodynamics in sensory processing and behaviours (Juusola et al., 2017; Kemppainen et al., 2022), emphasising their crucial role in enhancing perception and generating reliable neural representations of the variable world. Additionally, we propose underlying representational rules and general mechanisms governing morphodynamic sampling and information processing, to augment intelligence and cognition. We hope these ideas will pave the way for new insights and avenues in neuroscience research and our understanding of behaviour.

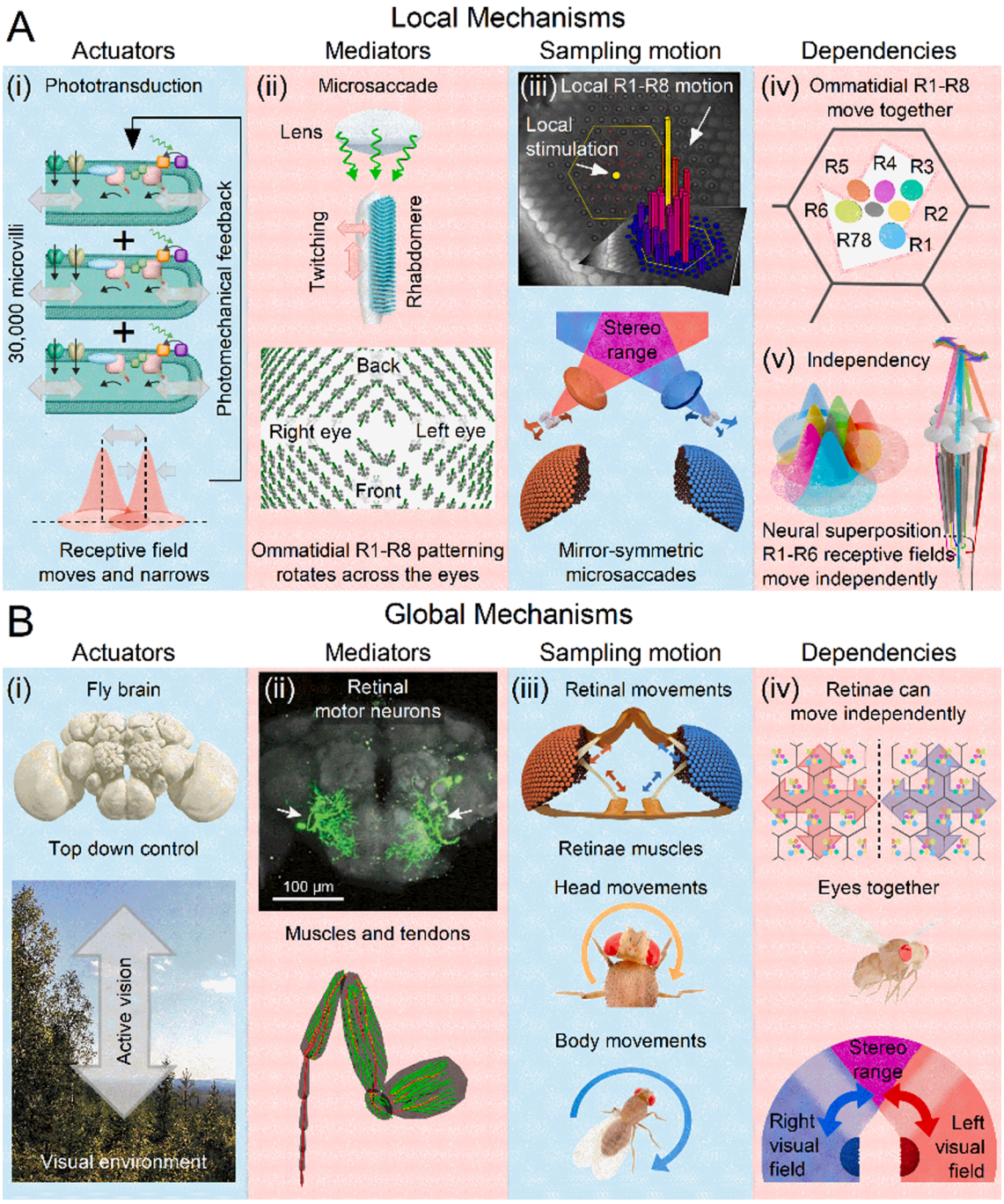
2. Sensing requires motion, and moving sensors improve sensing

The structure and function of sense organs have long been recognised as factors that limit the quantity and variety of information they can gather (Barlow and Rosenblith, 1961; Land, 1997; Laughlin et al., 1998). However, a more recent insight reveals that the process of sensing itself is an active mechanism, utilising bursty or saccadic movements to enhance information sampling (Chittka and Skorupski, 2017; Fenk et al., 2022; Gomez-Marin et al., 2011; Guiraud et al., 2018; Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022; Nityananda et al., 2014; Schilstra and Van Hateren, 1999; Smear et al., 2011; Sorribes et al., 2011; van Hateren and Schilstra, 1999; Vasas and Chittka, 2019) (Fig. 1). These movements encompass molecular, sensory cell, whole organ, head, and body motions, collectively and independently enhancing perception and behaviour. Box 1 introduces and summarises the general structure–function relationships of these motion-driven local and global image sampling mechanisms in active vision, using *Drosophila* as an example.

Because compound eyes extend from the rigid head exoskeleton, appearing stationary to an outside observer, the *prima facie* is that their inner workings would also be immobile (Exner, 1891; Land, 1997; Laughlin, 1989). Therefore, as the eyes' ommatidial faceting sets their photoreceptor spacing, the influential static theory of compound eye optics postulates that insects can only see a "pixelated" low-resolution image of the world. According to this traditional static viewpoint, the ommatidial grid limits the granularity of the retinal image and visual acuity. Resolving two stationary objects requires at least three photoreceptors, and this task becomes more challenging when objects are in motion, further reducing visual acuity. The presumed characteristics associated with small static compound eyes, including large receptive fields, slow integration times, and spatial separation of photoreceptors, commonly attributed to spherical geometry, contribute to motion blur that impairs the detailed resolution of moving objects within the visual field (Land, 1997). As a result, male *Drosophila* relying on coarse visual information face a dilemma, for example, in distinguishing between a receptive female fly and a hungry spider. To accurately differentiate, the male must closely approach the subject to detect distinguishing characteristics such as body shape, colour patterns, or movements. In this context, the difference between sex and death may hinge on an invisible line. (Note: This example highlights the importance of detailed

Box 1

Motion-Driven Image Sampling in Morphodynamic Active Vision. This text box graphically illustrates two fundamental sampling mechanisms that enhance vision through motion, using *Drosophila* as a model organism: (**A**) local sampling at the level of individual photoreceptors ("single-pixel") and (**B**) global sampling across the entire retinal matrix (whole-matrix). These interactive processes, which jointly affect the eyes' spatiotemporal resolution, stereoscopic range and adaptive capabilities, likely co-evolved to optimise visual perception and behaviour in dynamic natural environments.



(**A**) **Local Microsaccadic Image Sampling**. The photomechanical movement of R1-8 photoreceptors within an ommatidium enhances vision through morphodynamic sampling mechanisms:

(i) ***Photomechanical Receptive Field Scanning Motion***: Each photoreceptor's microvillar phototransduction reactions generate rapid contractions in response to light intensity changes, causing the photoreceptor's waveguide, the rhabdomere (containing 30,000 microvilli), to twitch (Hardie and Franze, 2012; Hardie and Juusola, 2015; Juusola et al., 2017) (grey double-headed arrows). These twitches create microsaccades that dynamically shift and narrow the photoreceptor's receptive field (Kemppainen et al., 2022) (red Gaussian). Unlike uniform, reflex-like contractions, microsaccades are actively regulated and continuously adjust photon sampling dynamics. This auto-

regulation optimises photoreceptors' receptive fields in response to environmental light changes to maximise information capture (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022). These dynamics rapidly adapt to ongoing light exposure, varying with both light intensity (dim vs bright conditions) and contrast type (positive for light increments, negative for light decrements) (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022). From a sampling theory perspective, photoreceptor microsaccades constitute a form of ultrafast, morphodynamic active sampling.

(ii) ***Local Directionality***: During a photomechanical microsaccade, photoreceptors contract axially (up-down arrow), moving away from the lens to narrow the receptive field while swinging sideways (left–right arrow) in a direction specific to their eye location, moving the receptive field (Kemppainen et al., 2022; Kemppainen et al., 2022). These lateral movements are predetermined during development as the ommatidial R1-8 photoreceptor alignment gradually rotates across the eyes (Kemppainen et al., 2022; Kemppainen et al., 2022), forming a diamond shape (with green lines indicating the rotation axis).

(iii) ***Insularity, Symmetry and Adaptability***: Local pinhole light stimulation (yellow dot) triggers microsaccades only in the photoreceptors of the illuminated ommatidia (yellow and red bars), while the photoreceptors in the neighbouring ommatidia (dark blue bars) remain still (Kemppainen et al., 2022). The left and right eyes show mirror-symmetric microsaccade directions (Kemppainen et al., 2022; Kemppainen et al., 2022), but local microsaccades themselves are not uniform (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022). Their speed and magnitude adapt to ambient light changes, becoming faster and shorter in brighter environments, indicating light-intensity dependency (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022).

(iv) ***Collective Motion*:** Within an ommatidium, R1-8 photoreceptor movements are interdependent. When one photoreceptor is activated by light, all R1-8 photoreceptors move together in a unified direction (Kemppainen et al., 2022). This coordinated motion likely arises from the photoreceptors' structural pivoting and the linkage of their rhabdomere tips to the ommatidial cone cells via adherens junctions (Juusola et al., 2017; Tepass and Harris, 2007). If all photoreceptors are activated, their combined microsaccades produce a larger collective movement (Kemppainen et al., 2022). A local UV light stimulus activating all R1-6 photoreceptors and R7 results in the largest microsaccades (Kemppainen et al., 2022).

(v) ***Asymmetry and Tiling*:** The asymmetric arrangement of R1-8 photoreceptors around the ommatidium lens causes R1-6 photoreceptors' receptive fields (coloured Gaussians), pooled from neighbouring ommatidia, to tile the visual space over-completely(Kemppainen et al., 2022; Pick, 1977) and move independently (correspondingly coloured arrows) in slightly different directions during synaptic transmission to large monopolar cells (Kemppainen et al., 2022).

(B) Global Image Sampling Movements: *Drosophila* uses retinal, head, and body movements to adapt and enhance its vision in response to behavioural needs and environmental changes.

(i) ***Top-Down Control*:** During closed-loop interactions with the environment, the fly brain exerts global control over visual information, enabling attentive perception (Chittka and Spaethe, 2007; Nityananda and Chittka, 2015; Tang and Juusola, 2010; Tang, Wolf, Xu, & Heisenberg, 2004; van Swinderen, 2011) and adaptive behaviours. This is exemplified in tethered *Drosophila* flight, where competing visual motion stimuli presented to the left and right eyes result in neural activity in the optic lobes, measured via extracellular electrodes, being enhanced on the selected side and suppressed on the opposite side, despite the visual input to both eyes remaining unchanged (Tang and Juusola, 2010).

(ii) ***Goal-Directed Behaviours***: The fly brain coordinates translational, rotational (Geurten et al., 2014) and vergence movements(Fenk et al., 2022) through retinal motoneurons and effector neurons that control muscles, ligaments, and tendons.

(iii) ***Self-Motion-Induced Optic Flow***: Retinal, head, and body movements, including saccades (Blaj and van Hateren, 2004; Geurten et al., 2014; van Hateren and Schilstra, 1999) and vergence (Fenk et al., 2022; Franceschini and Taddei-Ferretti, 1998; Franceschini et al., 1995), shift the entire retina, refreshing neural images across the visual field and preventing perceptual fading due to fast adaptation. The interplay between these global movements and (**A**) orientation-sensitive photoreceptor microsaccades generates complex spatiotemporal sampling dynamics. While microsaccades can independently enhance neural responses to local visual changes, whole retina movements rely on this interaction for full effectiveness. Each retinal movement alters the photoreceptor light input (Kemppainen et al., 2022), with moving scenes triggering photomechanical microsaccades – rippling wave patterns synchronised with contrast changes – across the retina, except in complete darkness or uniform, zero-contrast environments.

(iv) ***Coordinated Adjustments and Activity State*:** Although the left and right compound eyes are fixed together on the head cuticle, retinal muscles enable the left and right retinae (illustrated by the left and right ommatidial matrix) to move independently (Fenk et al., 2022) (red and blue four-headed arrows). This independent retinal motion provides precise control during an attentive viewing (Fenk et al., 2022; Tang and Juusola, 2010; Tang et al., 2004), including optokinetic retinal tracking and other behaviours. For example, by pulling the retinae inward (convergence) or outward (divergence), these muscles can adjust the number of frontal photoreceptors involved in stereopsis, dynamically altering the eyes' stereo range while preserving the integrity of the compound eyes' lens surface and surrounding exoskeleton. Interestingly, whole-retina movements, driven by retinal motor neuron activity, are seldom observed in intact, fully immobilised, head-fixed *Drosophila*, such as during intracellular electrophysiological recordings or in vivo photoreceptor imaging (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022). Instead, one occasionally notes slow retinal drifting, likely due to changes in muscle tone affecting retinal tension, which necessitates recentring the light stimulus (Juusola et al., 2017). However, the whole-retina movements become more frequent and pronounced when the flies are less restricted and actively engaged in stimulus tracking or visual behaviours, such as during tethered flight or while walking on a trackball (Fenk et al., 2022; Franceschini and Taddei-Ferretti, 1998; Franceschini et al., 1995). These findings align with previous observations from two-photon calcium imaging (Chiappe et al., 2010; Chiappe, 2023; Fujiwara et al., 2017; Fujiwara et al., 2022; Maimon et al., 2010) and extracellular electrophysiology (Grabowska et al., 2020; Tang and Juusola, 2010; van Swinderen, 2011), which demonstrate that the fly's behavioural state influences neural activity in the fly brain's visual processing centres.

resolution in minimising uncertainty. However, flies' decision-making during social behaviours is unlikely to depend solely on a single sensory modality. Instead, it is holistic and context-, experiment-, and state-dependent (Agrawal and Dickinson, 2019; Agrawal et al., 2014; Pan et al., 2012; Bath et al., 2014; Inagaki et al., 2014; Clowney et al., 2015; Nordström et al., 2006; Ribeiro et al., 2018; Schretter et al., 2024; Sten et al., 2021), integrating multisensory inputs – tactile, chemosensory, auditory, and visual – along with learned and genetic information, as will be discussed later.).

Recent studies on *Drosophila* have challenged the notion that fixed factors such as photoreceptor spacing, integration time, and receptive field size solely determine visual acuity (Juusola et al., 2017;

Kemppainen et al., 2022). Instead, these characteristics are dynamically regulated by photoreceptor photomechanics (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022), leading to significant improvements in vision through morphodynamic processes. In the following subsections, we begin by explaining how microsaccadic movements of photoreceptors enable hyperacute image sampling (Fig. 2), phasic image contrast enhancement (Fig. 3), information maximisation during saccadic behaviours (Fig. 4), hyperacute stereovision (Fig. 5), and antialiased vision (Fig. 6). We then relate these predominantly *local* image sampling dynamics to the *global* movements of the retina, head, and entire animal in goal-oriented visual behaviours. Finally, we discuss the generic benefits of neural morphodynamics. Through specific examples, we explore how morphodynamic information sampling and processing adapt to maximise information allocation in neural channels (Fig. 7). We also link multiscale observations with *Gedankenexperimente* to envision how these ultrafast phasic processes synchronise the brain's neural representation of the external world with its dynamic changes (Fig. 8), thereby enhancing cognitive abilities and efficiency. Some of these concepts related to neural computations, intelligence, and future technologies are further explored in **Text** Boxes 2-4.

2.1. Photoreceptor microsaccades enhance vision

Intricate experiments (Fig. 2**A**) have revealed that photoreceptors rapidly move in response to light intensity changes (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022). Referred to as high-speed photomechanical microsaccades (Juusola et al., 2017; Kemppainen et al., 2022), these movements, which resemble a complex piston motion (Fig. 2**B**), occur in less than 100 ms and involve simultaneous axial recoil and lateral swinging of the photoreceptors within a single ommatidium. These local morphodynamics result in adaptive optics (Fig. 2**C**), enhancing spatial sampling resolution and sharpening moving light patterns over time by narrowing and shifting the photoreceptors' receptive fields (Juusola et al., 2017; Kemppainen et al., 2022).

To understand the core concept and its impact on compound eye vision, let us compare the photoreceptors' receptive fields to image pixels in a digital camera (Fig. 2**E**). Imagine shifting the camera sensor, capturing two consecutive images with a 1/2-pixel displacement. This movement effectively doubles the spatial image information. By integrating these two images over time, the resolution is significantly improved. However, if a pixel moves even further, it eventually merges with its neighbouring pixel (provided the neighbouring pixel remains still and does not detect changes in light). As a result of this complete pixel fusion, the acuity decreases since the resulting neural image will contain fewer pixels. Therefore, by restricting photoreceptors' microscanning to the interommatidial angle, *Drosophila* can effectively time-integrate a neural image that exceeds the optical limits of its compound eyes.

2.2. Microsaccades are photomechanical adaptations in phototransduction

Drosophila photoreceptors exhibit a distinctive toothbrush-like morphology characterised by their "bristled" light-sensitive structures known as rhabdomeres. In the outer photoreceptors (R1-6), there are approximately 30,000 bristles, called microvilli, which act as photon sampling units (Fig. 2**D**) (Hardie and Franze, 2012; Juusola et al., 2017; Kemppainen et al., 2022). These microvilli collectively function as a waveguide, capturing light information across the photoreceptor's receptive field (Kemppainen et al., 2022; Kemppainen et al., 2022). Each microvillus compartmentalises the complete set of phototransduction cascade reactions (Hardie and Juusola, 2015), contributing to the refractive index and waveguide properties of the rhabdomere (Stavenga, 2003). The phototransduction reactions within rhabdomeric microvilli of insect photoreceptors generate ultra-fast contractions of the whole rhabdomere caused by the PLC-mediated cleavage of PIP_2 headgroups (InsP3) from the microvillar membrane (Hardie and Franze, 2012; Hardie and Juusola, 2015). These photomechanics rapidly adjust the photoreceptor, enabling it to dynamically adapt its light input as the receptive field reshapes and interacts with the surrounding environment. Because photoreceptor microsaccades directly result from phototransduction reactions (Hardie and Franze, 2012; Hardie and Juusola, 2015; Juusola et al., 2017; Kemppainen et al., 2022), they are an inevitable consequence of compound eye vision. Without microsaccades, insects with microvillar photoreceptors would be blind (Hardie and Franze, 2012; Hardie and Juusola, 2015; Juusola et al., 2017; Kemppainen et al., 2022).

Insects possess an impressively rapid vision, operating approximately 3 to 15 times faster than our own. This remarkable ability stems from the microvilli's swift conversion of captured photons into brief unitary responses (Fig. 2**D**; also known as quantum bumps (Hardie and Juusola, 2015) and their ability to generate photomechanical micromovements (Hardie and Franze, 2012; Juusola et al., 2017) (Fig. 2**C**). Moreover, the size and speed of microsaccades adapt to the microvilli population's refractory photon sampling dynamics (Juusola et al., 2017; Song et al., 2012) (Fig. 2**D**). As light intensity increases, both the quantum efficiency and duration of photoreceptors' quantum bumps decrease (Juusola and Hardie, 2001; Song et al., 2012), resulting in more transient microsaccades (Juusola et al., 2017; Kemppainen et al., 2022). These adaptations extend the dynamic range of vision (Juusola and Song, 2017; Song et al., 2012) and enhance the detection of environmental contrast changes (Juusola et al., 2017; Song and Juusola, 2014), making visual objects highly noticeable under various lighting conditions. Consequently, *Drosophila* can perceive moving objects across a wide range of velocities and light intensities, surpassing the resolution limits of the static eye's pixelation by 4–10 times (Fig. 2**E**; the average inter-ommatidial angle, $\varphi \approx 5^{\circ}$) (Juusola et al., 2017; Kemppainen et al., 2022).

Morphodynamic adaptations involving photoreceptor microvilli play a crucial role in insect vision by enabling rapid and efficient visual information processing. These adaptations lead to contrast-normalised (Fig. 2**D**) and more phasic photoreceptor responses, achieved through significantly reduced integration time (Juusola et al., 2017; Song and Juusola, 2014; Song et al., 2021). Evolution further refines these dynamics to match species-specific visual needs (Fig. 2**E**). For example, honeybee microsaccades are smaller than those of *Drosophila* (Kemppainen et al., 2022), corresponding to the positioning of honeybee photoreceptors farther away from the ommatidium lenses. Consequently, reducing the receptive field size and interommatidial angles in honeybees is likely an adaptation that allows optimal image resolution during scanning (Kemppainen et al., 2022). Similarly, fast-flying flies such as houseflies and blowflies, characterised by a higher density of ommatidia in their eyes, are expected to exhibit smaller and faster photoreceptor microsaccades compared to slower-flying *Drosophila* with fewer and less densely packed ommatidia (Kemppainen et al., 2022). This adaptation enables the fast-flying flies to capture visual information with higher velocity (Gonzalez-Bellido et al., 2011; Juusola, 1993; Song and Juusola, 2014; Song et al., 2012) and resolution, albeit at a higher metabolic cost (Song and Juusola, 2014).

2.3. Microsaccades maximise information during saccadic behaviours

Photoreceptors' microsaccadic sampling likely evolved to align with animals' saccadic behaviours, maximising visual information capture (Juusola et al., 2017; Kemppainen et al., 2022). Saccades are utilised by insects and humans to explore their environment (Fig. 1**I-L**), followed by fixation periods where the gaze remains relatively still (Land, 2019). Previously, it was believed that detailed information was only sampled during fixation, as photoreceptors were thought to have slow integration times, causing image blurring during saccades (Land, 2019). However, fixation intervals can lead to perceptual fading through powerful

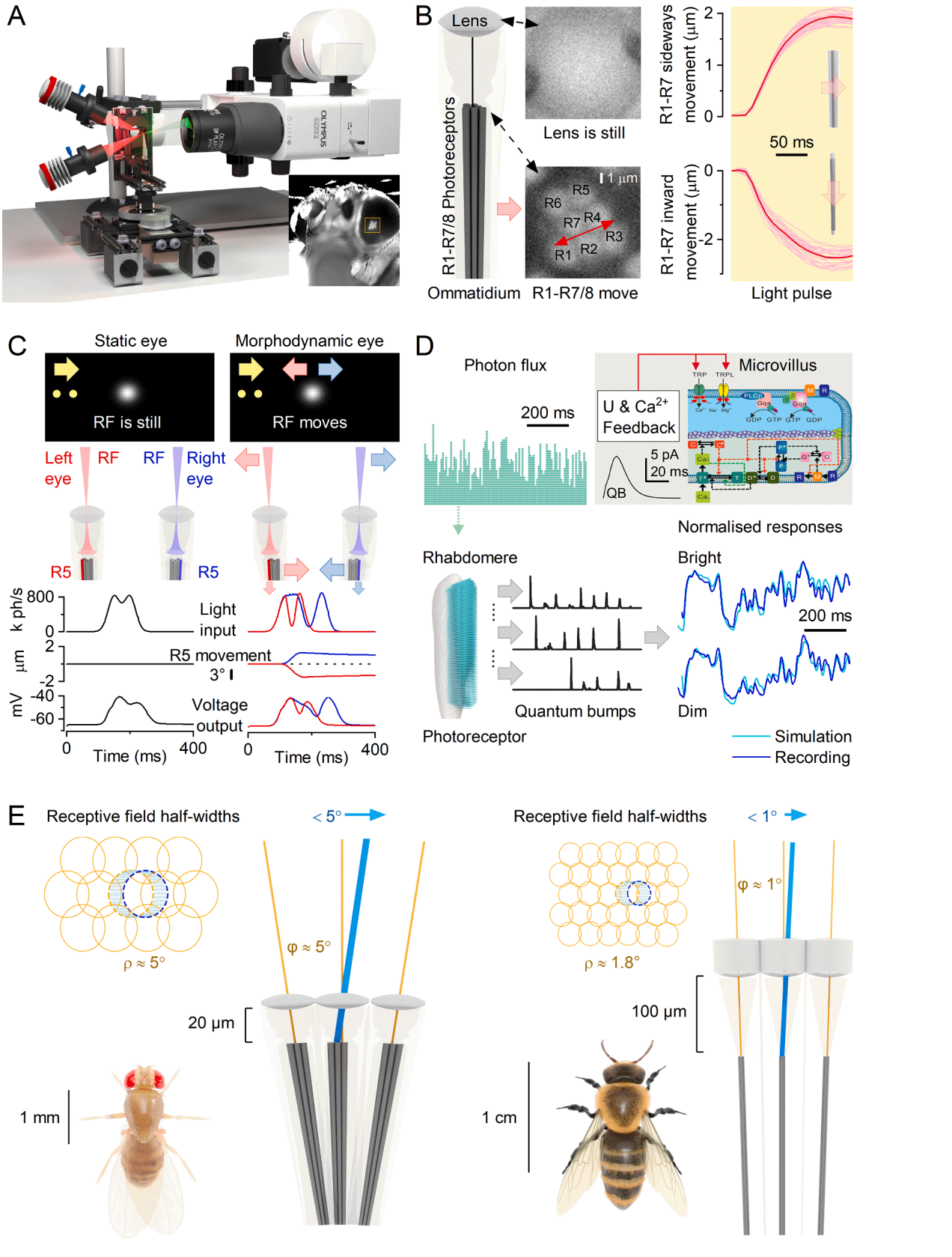


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Fig. 2. Photomechanical photoreceptor microsaccades enhance insect vision through adaptive compound eye optics. (A) High-speed infrared deep-pseudopupil microscopy (Kemppainen et al., 2022; Kemppainen et al., 2022) uncovers the intricate movement dynamics and specific directions of light-induced photoreceptor microsaccades across the compound eyes in living *Drosophila*. Fully immobilising the flies inside a pipette tip minimises whole-retina movements, allowing one to record photoreceptor microsaccade dynamics in isolation (Kemppainen et al., 2022; Kemppainen et al., 2022). (B) During a microsaccade within an ommatidium, the R1-R7/8 photoreceptors undergo rapid axial (inward) contraction and sideways movement along the R1-R2-R3 direction, executing a complex piston motion (Kemppainen et al., 2022; Kemppainen et al., 2022). Meanwhile, the lens positioned above them, as an integral component of the rigid exoskeleton, remains stationary (Juusola et al., 2017). (C) When a moving light stimulus, such as two bright dots, traverses a photoreceptor's (shown for R5) receptive field (RF), the photoreceptor rapidly contracts away from the lens, causing the RF to narrow (Juusola et al., 2017; Kemppainen et al., 2022). Simultaneously, the photoreceptor's swift sideways movement, aided by the lens acting as an optical lever, results in the RF moving in the opposite direction (of about 40-60°/s, illustrated here for movement with or against the stimuli). As a result, in a morphodynamic compound eye, the photoreceptor responses (depicted by blue and red traces) can detect finer and faster changes in moving stimuli than what the previous static compound eye theory predicts (represented by black traces). (D) Microsaccades result from photomechanical processes involving refractory photon sampling dynamics within the 30,000 microvilli (Hardie and Franze, 2012; Hardie and Juusola, 2015; Juusola et al., 2017; Kemppainen et al., 2022), which comprise the light-sensitive part of a photoreceptor known as the rhabdomere. Each microvillus encompasses the complete phototransduction cascade, enabling the conversion of successful photon captures into elementary responses called quantum bumps. This photomechanical refractory sampling mechanism empowers photoreceptors to consistently estimate changes in environmental light contrast across a wide logarithmic intensity range. The intracellularly recorded morphodynamic quantal information sampling and processing (represented by dark blue traces) can be accurately simulated under various light conditions using biophysically realistic stochastic photoreceptor sampling models (illustrated by cyan traces) (Juusola et al., 2017; Kemppainen et al., 2022; Song et al., 2012). (E) *Drosophila* photoreceptor microsaccades shift their rhabdomeres sideways by around 1–1.5 μm (maximum < 2 μm), resulting in receptive field movements of approximately 3–4.5° in the visual space. The receptive field half-widths of R1-6 photoreceptors cover the entire visual space, ranging from 4.5 to 6°. By limiting the micro-scanning to the interommatidial angle, *Drosophila* integrates a neural image that surpasses the optical limits of its compound eyes. Honeybee photoreceptor microsaccades shift their receptive fields by < 1°, smaller than the average receptive field half-width (~1.8°) at the front of the eye. This active sampling strategy in honeybees is similar to Drosophila and suggests that honeybee vision also surpasses the static pixelation limit of its compound eyes (Kemppainen et al., 2022). Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

adaptation, reducing visual information and potentially limiting perception to average light levels (Ditchburn and Ginsborg, 1952; Juusola et al., 2017; Riggs and Ratliff, 1952). Therefore, to maximise information capture, fixation durations and saccade speeds should dynamically adapt to the statistical properties of the natural environment (Juusola et al., 2017). This sampling strategy would enable animals to efficiently adjust their behavioural speed and movement patterns in diverse environments, optimising vision – for example, moving slowly in darkness and faster in daylight(Juusola et al., 2017).

To investigate this theory, researchers studied the body yaw velocities of walking fruit flies (Geurten et al., 2014) to sample light intensity information from natural images (Juusola et al., 2017) (Fig. 3). They found that saccadic viewing of these images improved the photoreceptors' information capture compared to linear or shuffled velocity walks (Juusola et al., 2017). This improvement was attributed to saccadic viewing generating bursty high-contrast stimulation, maximising the photoreceptors' ability to gather information. Specifically, the photomechanical and refractory phototransduction reactions of *Drosophila* R1-6 photoreceptors, associated with motion vision (Borst, 2009), were found to be finely tuned to saccadic behaviour for sampling quantal light information, enabling them to capture 2-to-4-times more information in a given time compared to previous estimates (Juusola and Hardie, 2001; Juusola et al., 2017).

Further analysis, utilising multiscale biophysical modelling (Song et al., 2021), investigated the stochastic refractory photon sampling by 30,000 microvilli (Juusola et al., 2017). For readers interested in more details, **Text** Box 2 graphically illustrates the basic principles of stochastic quantal refractory sampling. The findings revealed that the improved information capture during saccadic viewing can be attributed to the interspersed fixation intervals (Juusola and Song, 2017; Juusola et al., 2017). When fixating on darker objects, which alleviates microvilli refractoriness, photoreceptors can sample more information from transient light changes, capturing larger photon rate variations (Juusola et al., 2017). The combined effect of photomechanical photoreceptor movements and refractory sampling worked synergistically to enhance spatial acuity, reduce motion blur during saccades, facilitate adaptation during gaze fixation, and emphasise instances when visual objects crossed a photoreceptor's receptive field. Consequently, the encoding of high-resolution spatial information was achieved through the temporal mechanisms induced by physical motion (Juusola et al., 2017).

These discoveries underscore the crucial link between an animal's adaptation in utilising movements across different scales, ranging from nanoscale molecular dynamics to microscopic brain morphodynamics, to maximise visual information capture and acuity (Juusola et al., 2017). The new understanding from the *Drosophila* studies is that contrary to popular assumptions, neither saccades (Land, 1997) nor fixations (Ditchburn and Ginsborg, 1952) hinder the vision. Instead, they work together to enhance visual perception, highlighting the complementary nature of these active sampling movement patterns (Juusola et al., 2017).

2.4. *Left and right eyes' mirror-symmetric microsaccades phase-enhance moving objects*

When *Drosophila* encounters moving objects in natural environments, its left and right eye photoreceptor pairs generate microsaccadic movements that synchronise their receptive field scanning in opposite directions (Fig. 4) (Juusola et al., 2017; Kemppainen et al., 2022). To quantitatively analyse these morphodynamics, researchers utilised a custom-designed high-speed microscope system (Kemppainen et al., 2022), tailored explicitly for recording photoreceptor movements within insect compound eyes; an early prototype of this instrument is shown in Fig. 2**A**, while Video 1 demonstrates these experiments. Using infrared illumination, which flies cannot see (Kemppainen et al., 2022; Kemppainen et al., 2022; Sharkey et al., 2020; Wardill et al., 2012), the positions and orientations of photoreceptors in both eyes were measured, revealing mirror-symmetric angular orientations between the eyes and symmetry within each eye (Fig. 4**A**). It was discovered that a single point in space within the frontal region, where receptive fields overlap (Fig. 4**B**), is detected by at least 16 photoreceptors, eight in each (Kemppainen et al., 2022; Kemppainen et al., 2022). This highly ordered mirror-symmetric rhabdomere organisation, leading to massively overcomplete tiling of the eyes' binocular visual fields (Kemppainen et al., 2022) (Fig. 4**C**), challenges the historical belief that small insect eyes, such as those of *Drosophila*, are optically too coarse and closely positioned to support stereovision (Land, 1997).

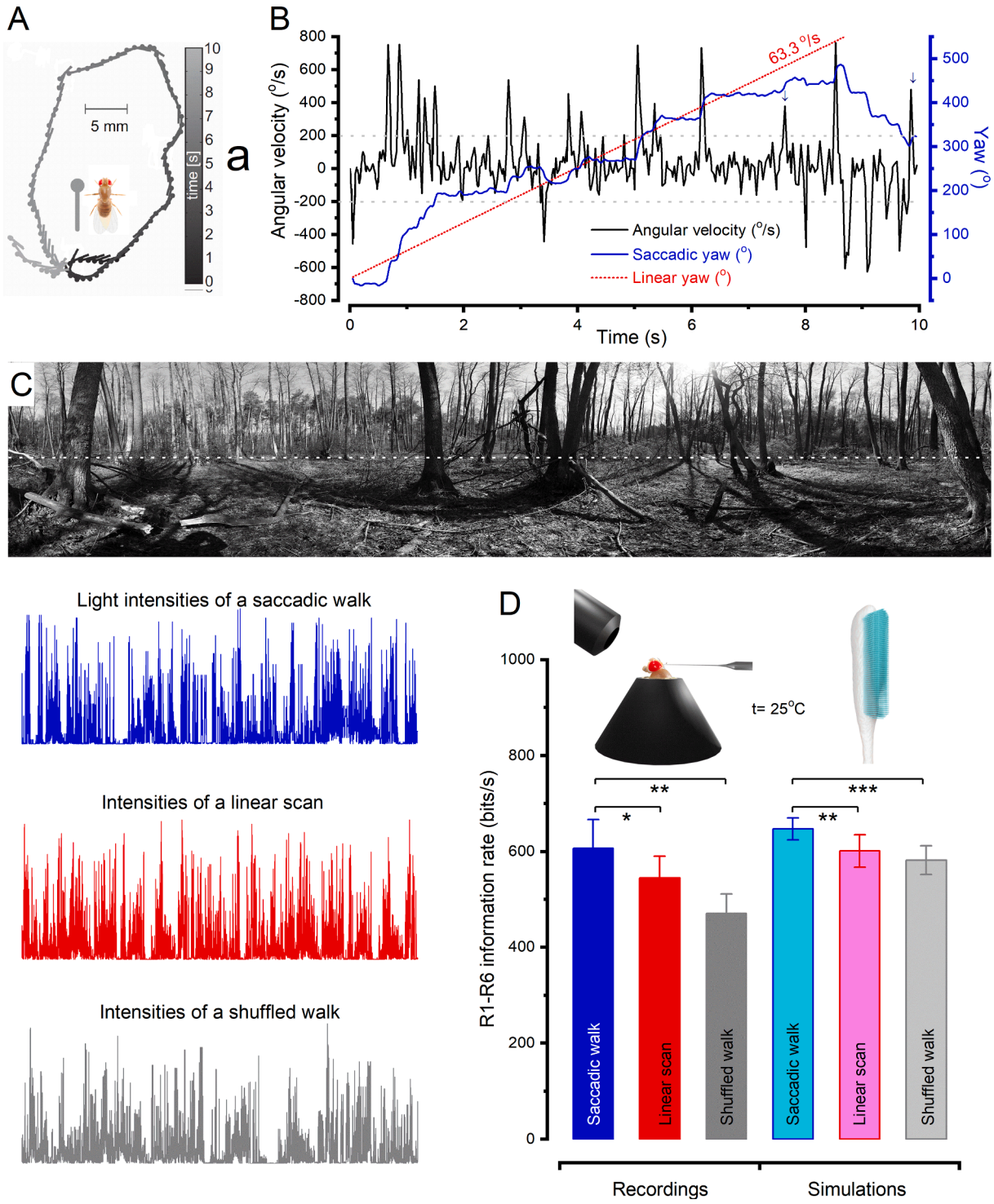

Fig. 3. Saccadic Turns and Fixation Periods Enhance Information Extraction in *Drosophila*. (A) A representative walking trajectory of a fruit fly (Geurten et al., 2014). (B) Angular velocity and yaw of the recorded walk. (C) A 360° natural scene utilised to generate three distinct time series of light intensity (Juusola et al., 2017). The dotted white line indicates the intensity plane employed during the walk. The blue trace represents a light intensity over time generated by overlaying the walking fly's yaw dynamics (A-B) onto the scene. The red trace corresponds to the time series of light intensity obtained by scanning the scene at the median velocity of the walk (linear: 63.3°/s). The grey trace depicts the time series of light intensity obtained using shuffled walking velocities. Brief saccades and longer fixation periods introduce burst-like patterns to the light input. (D) These light intensity time series were employed as stimuli in intracellular photoreceptor recordings and simulations using a biophysically realistic stochastic photoreceptor model. Both the recordings and simulations showed that saccadic viewing enhances information transmission in R1-6 photoreceptors, indicating that this mechanism has evolved with refractory photon sampling to maximise information capture from natural scenes (Juusola et al., 2017). Immobilising the flies (their head, proboscis and thorax) with beeswax (Juusola and Hardie, 2001; Juusola et al., 2016) in a conical holder minimises whole-retina movements (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022), enabling high signal-to-noise recording conditions to study photoreceptors' voltage responses to dynamic light stimulation (Juusola et al., 2017). Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

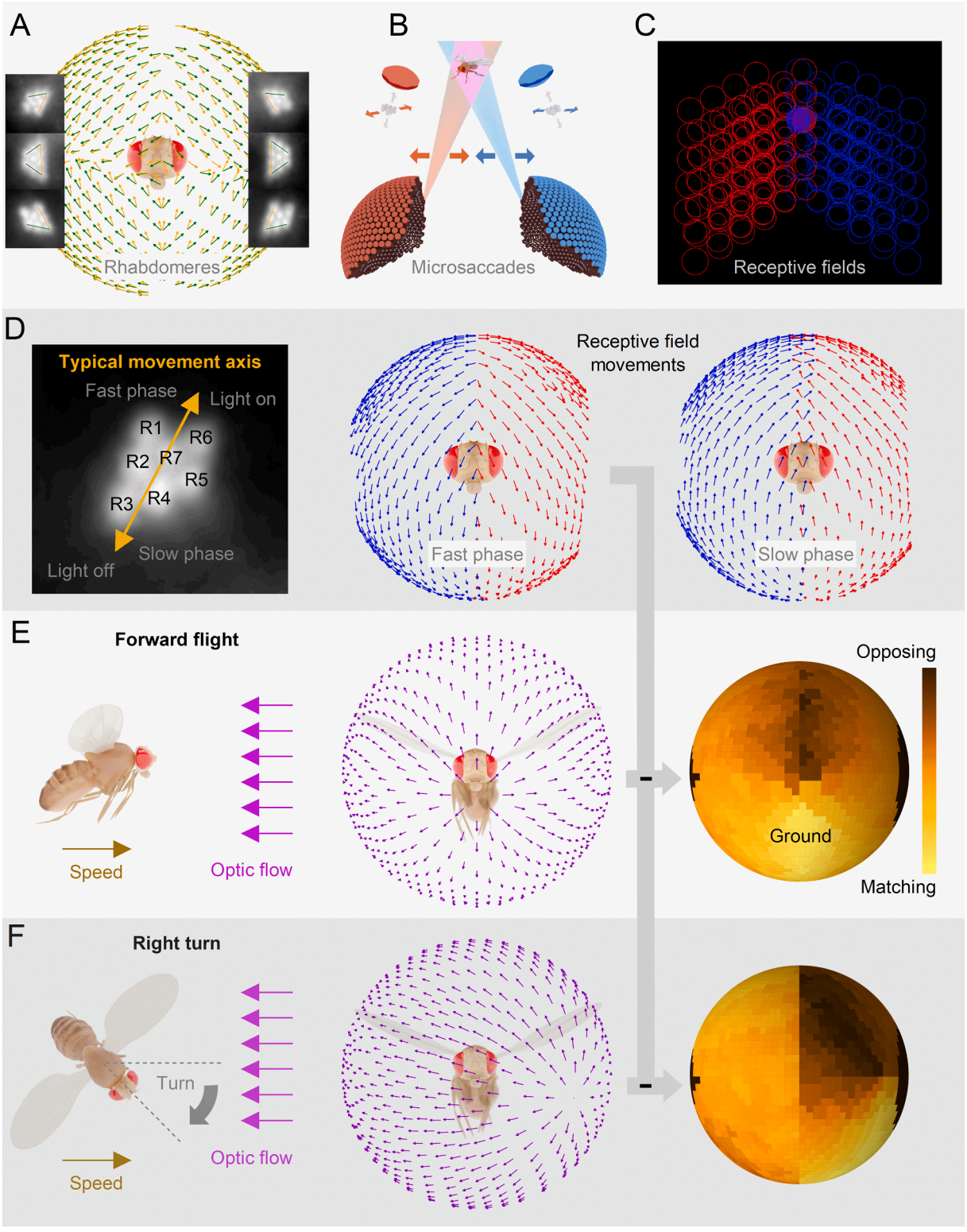

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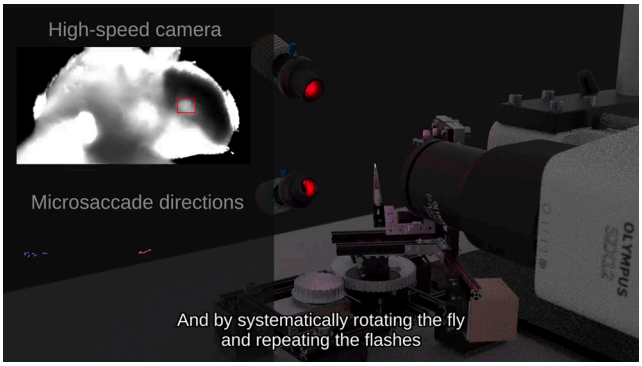
Fig. 4. The mirror-symmetric ommatidial photoreceptor arrangement and morphodynamics of the left and right eyes enhance detection of moving objects during visual behaviours. (A) The photoreceptor rhabdomere patterns (as indicated by their rotating orientation directions: yellow and green arrows) of the ommatidial left and right eyes (inset images) exhibit horizontal and ventral mirror symmetry, forming a concentrically expanding diamond shape(Franceschini and Kirschfeld, 1971; Kemppainen et al., 2022; Kemppainen et al., 2022). (B) When a moving object, such as a fly, enters the receptive fields (RFs) of the corresponding frontal left and right photoreceptors (indicated by red and blue beams), the resulting light intensity changes cause the photoreceptors to contract mirror-symmetrically. (C) The half-widths of the frontal left and right eye R6 photoreceptors' RFs (disks), projected 5 mm away from the eyes (Kemppainen et al., 2022). Red circles represent the RFs of neighbouring photoreceptors in the left visual field, blue in the right. (D) Contraction (light-on) moves R1-R7/8 photoreceptors (left) in R3-R2-R1 direction (fast-phase), recoil (light-off) returns them in opposite R1-R2-R3 direction (slow-phase) (Kemppainen et al., 2022; Kemppainen et al., 2022). The corresponding fast-phase (centre) and slow-phase (right) RF vector maps. (E) The fast-phase RF map compared to the forward flying fly's optic flow field (centre), as experienced with the fly head upright (Kemppainen et al., 2022). Their difference is shown on the right. The fast-phase matches the ground flow (light yellow pixels), while the opposite slow-phase (dark yellow pixels) matches the sky flow (Kemppainen et al., 2022). (F) During yaw rotation, the mirror-symmetric movement of the photoreceptor RFs in the left and right eyes enhances the binocular contrast differences in the surrounding environment (sample visualisation as panel E). Immobilising the flies inside a pipette tip, as was done for these recordings, minimises whole-retina movements, allowing for the isolated study of photoreceptor microsaccade dynamics (Kemppainen et al., 2022; Kemppainen et al., 2022). Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Video 1.

By selectively stimulating the rhabdomeres with targeted light flashes, researchers determined the specific photomechanical contraction directions for each eye's location (Fig. 4**D**). Analysis of the resulting microsaccades enabled the construction of a 3D-vector map encompassing the frontal and peripheral areas of the eyes. These microsaccades exhibited mirror symmetry between the eyes and aligned with the rotation axis of the R1-R2-R3 photoreceptor of each ommatidium (Fig. 4**D**, left), indicating that the photoreceptors' movement directions were predetermined during development (Fig. 4**A**) (Kemppainen et al., 2022; Kemppainen et al., 2022). Strikingly, the 3D-vector map representing the movements of the corresponding photoreceptor receptive fields (Fig. 4**D**) coincides with the optic flow-field generated by the fly's forward thrust (Fig. 4**E**) (Kemppainen et al., 2022; Kemppainen et al., 2022). This alignment provides microsaccade-enhanced detection and resolution of moving objects (cf. Fig. 4**C**) across the extensive visual fields of the eyes (approximately 360°), suggesting an evolutionary optimisation of fly vision for this intriguing capability.

The microsaccadic receptive field movements comprise a fast phase (Fig. 4**D**, left) aligned with the flow-field direction during light-on (Fig. 4**D**, middle), followed by a slower phase in the opposite direction during light-off (Fig. 4**D**, right). When a fly is in forward flight with an upright head (Fig. 5**E**, left and middle), the fast and slow phases reach equilibrium (Fig. 4**E**, right). The fast phase represents "ground-flow," while the slower phase represents "sky-flow." In the presence of real-world structures, locomotion enhances sampling through a push–pull mechanism. Photoreceptors transition between fast and slow phases, thereby collectively improving neural resolution over time (Kemppainen et al., 2022) (Fig. 2**C**). Fast microsaccades are expected to aid in resolving intricate visual clutter, whereas slower microsaccades enhance the perception of the surrounding landscape and sky (Kemppainen et al., 2022). Moreover, this eye-location-dependent orientation-tuned bidirectional visual object enhancement makes any moving object deviating from the prevailing self-motion-induced optic flow field stand out. Insect brains likely utilise the resulting phasic neural image contrast differences to detect or track predator movements or conspecifics across the eyes' visual fields. For example, this mechanism could help a honeybee drone spot and track the queen amidst a competing drone swarm (Woodgate et al., 2021), enabling efficient approach and social interaction.

Rotation (yaw) (Fig. 4**F**, left and middle) further enhances binocular contrasts (Fig. 4**F**, right), with one eye's phases synchronised with field rotation while the other eye's phases exhibit the reverse pattern (Kemppainen et al., 2022). Many insects, including bees and wasps, engage in elaborately patterned learning or homing flights, involving fast saccadic turns and bursty repetitive wave-like scanning motion when leaving their nest or food sources (Boeddeker et al., 2010; Schulte et al., 2019) (Fig. 4**G**). Given the mirror-symmetricity and ultrafast photoreceptor microsaccades of bee eyes(Kemppainen et al., 2022), these flight patterns are expected to drive enhanced binocular detection of behaviourally relevant objects, landmarks, and patterns, utilising the phasic differences in microsaccadic visual information sampling between the two eyes (Juusola et al., 2017; Kemppainen et al., 2022). Thus, learning flight behaviours might make effective use of optic-flow-tuned and morphodynamically enhanced binocular vision, enabling insects to navigate and return to their desired locations successfully.

2.5. *Mirror-symmetric microsaccades enable hyperacute stereovision*

Crucially, *Drosophila* uses mirror-symmetric microsaccades to sample the three-dimensional visual world, enabling the extraction of depth information (Fig. 5). This process entails comparing the resulting morphodynamically sampled neural images from its left and right eye photoreceptors (Kemppainen et al., 2022). The disparities in x- and y-coordinates between corresponding "pixels" provide insights into scene depth. In response to light intensity changes, the left and right eye photoreceptors contract mirror-symmetrically, narrowing and sliding their receptive fields in opposing directions, thus shaping neural responses (Fig. 5**A**; also see Fig. 2**C**) (Juusola et al., 2017; Kemppainen et al., 2022). By cross-correlating these photomechanical responses between neighbouring ommatidia, the *Drosophila* brain is predicted to achieve a reliable stereovision range spanning from less than 1 mm to approximately 150 mm (Kemppainen et al., 2022). The crucial aspect lies in utilising the responses' phase differences as temporal cues for perceiving 3D space (Fig. 5**A, B**). Furthermore, researchers assessed if a static *Drosophila* eye model with immobile photoreceptors could discern depth (Kemppainen et al., 2022). These calculations indicate that the lack of scanning activity by the immobile photoreceptors and the small distance between the eyes (Fig. 5**A**, $k = 440\,\mu m$) would only enable a significantly reduced depth perception range, underlining the physical and evolutionary advantages of moving photoreceptors in depth perception.

Furthermore, optical calculations using the Fourier beam propagation (Hoekstra, 1997; Kemppainen et al., 2022) – which models in reverse how light beams pass through the photoreceptor rhabdomeres and the ommatidium lens into the visual space – have confirmed and

expanded upon Pick's earlier and often overlooked discovery(Pick, 1977). This analysis reveals that the receptive fields of R1-6 photoreceptors from neighbouring fly ommatidia, which feed information to the first visual interneurons (Large Monopolar Cells, LMCs), do not overlap perfectly. Instead, due to variations in the sizes of R1-6 rhabdomeres, their distances from the ommatidial centre, and the non-spherical shape of the eye, their receptive fields tile a small area in the visual space over-completely in neural superposition (Kemppainen et al., 2022; Pick, 1977) (Fig. 5**B**; see also Fig. 4**C**). In living flies, this situation becomes more complex and interesting as these receptive fields move and narrow independently, as illustrated through computer simulations in Video 2, following the morphodynamic rules of their photoreceptor microsaccades (Kemppainen et al., 2022; Kemppainen et al., 2022) (Fig. 5**B** and **Text Box 1A**). Consequently, this coordinated morphodynamic sampling motion is reflected in the orientation-sensitive hyperacute LMC responses, as observed in high-speed calcium imaging of L2 monopolar cell axon terminals (Kemppainen et al., 2022) (Fig. 5**B**).

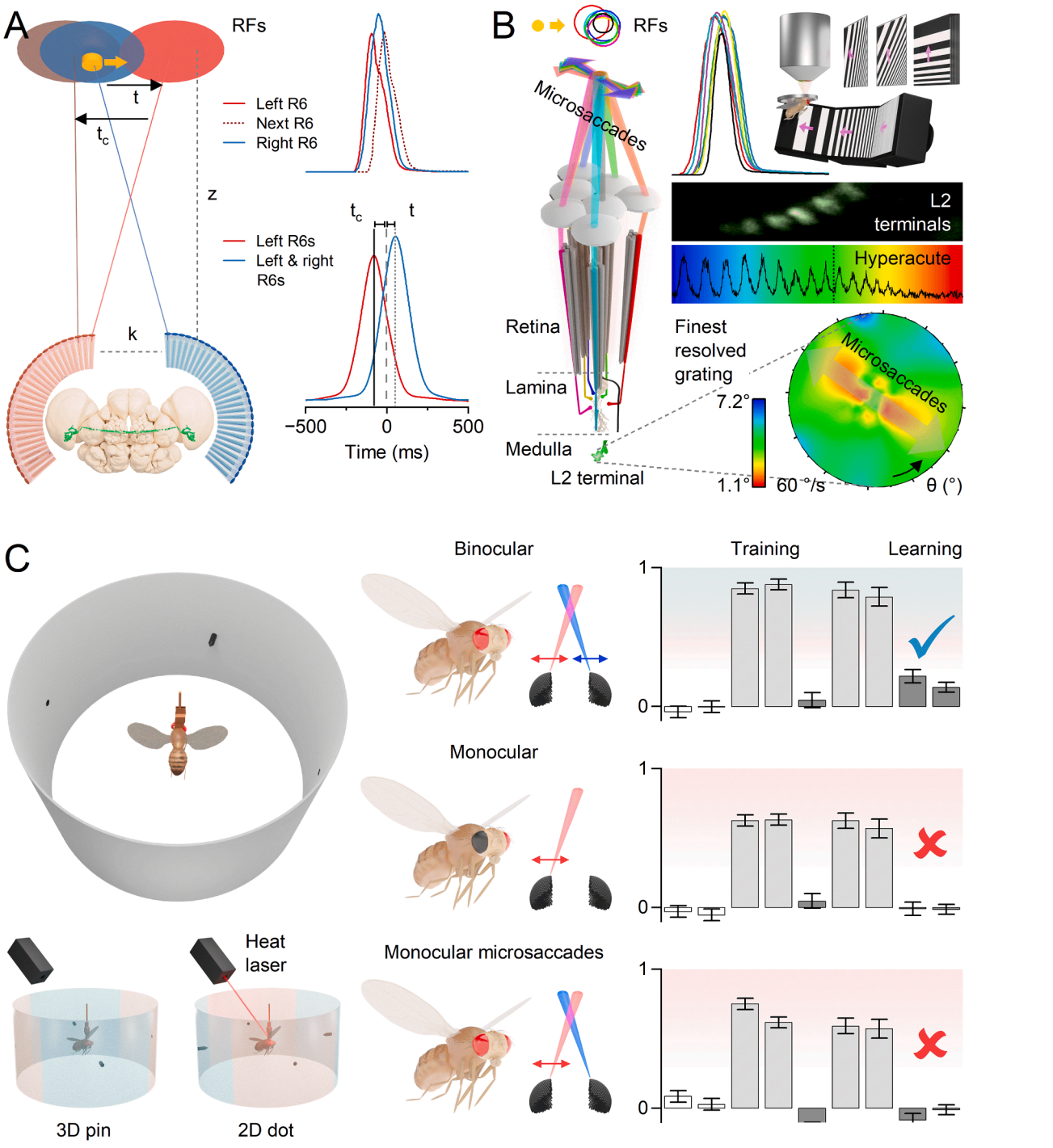


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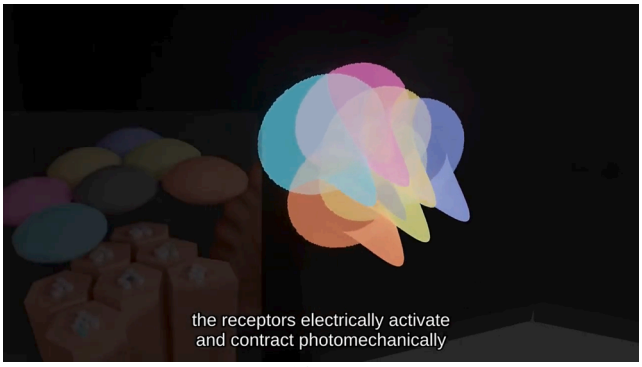
Fig. 5. *Drosophila* visual behaviours exhibit hyperacute 3D vision, aligning with morphodynamic compound eye modelling. (A) Drosophila compound eyes' depth perception constraints and the computations for morphodynamic triangulation of object depth (z) (Kemppainen et al., 2022). k is the distance between the corresponding left and right eye photoreceptors, and t is their time-delay. t_c is the time-delay between the neighbouring photoreceptors in the same eye. The left eye is represented by the red receptive field (RFs), while the right eye is represented by the blue RF. Simulated voltage responses (top) of three morphodynamically responding R6-photoreceptors when a 1.7° x 1.7° object (orange) moves across their overlapping RFs at a speed of 50°/s and a distance of 25 mm. The corresponding binocular cross-correlations (bottom), which represents the depth information, likely occur in the retinotopically organised neural cartridges of the lobula optic lobe, where location-specific ipsi- and contralateral photoreceptor information is pooled (green LC14 neuron (Kemppainen et al., 2022). Time delays between the maximum correlations (vertical lines) and the moment the object crosses the RF centre of the left R6-photoreceptor (vertical dashed line). (B) In neural superposition wiring (Kirschfeld, 1973), the R1-6 photoreceptors originating from six neighbouring ommatidia sample a moving stimulus (orange dot). Their overlapping receptive fields (RFs; coloured rings) swiftly bounce along their predetermined microsaccade directions (coloured arrows; see also Fig. 4D) as the photoreceptors transmit information to large monopolar cells (LMC, specifically L1-L3, with L2 shown) and the lamina amacrine cells. While R7/8 photoreceptors share some information with R1 and R6 through gap junctions (Wardill et al., 2012) R7/8 establish synapses in the medulla. Simulations reveal the superpositional R1-R7/8s' voltage responses (coloured traces) with their phase differences when a 1.7° x 1.7° dot traverses their receptive fields at 100°/s (orange dot). 2-photon imaging of L2 terminals' Ca^{2+} -responses to a dynamically narrowing black-and-white grid that moves in different directions shows L2 monopolar cells generating hyperacute (<5°; cf. Fig. 2B-C, E) responses along the same microsaccade movement axis (coloured arrows) of the superpositioned photoreceptors that feed information to them (cf. Fig. 4). (C) In a visual learning experiment, a tethered, head-immobilised *Drosophila* flies in a flight simulator. The fly was positioned at the centre of a panoramic arena to prevent it from perceiving motion parallax cues (Kemppainen et al., 2022). The arena features two hyperacute dots placed 180° apart and two equally sized 3D pins positioned perpendicular to the dots. The fly generates subtle yaw torque signals to indicate its intention to turn left or right, allowing it to explore the visual objects within the arena. These signals are used to rotate the arena in the opposite direction of the fly's intended turns, establishing a synchronised feedback loop. During the training phase, a heat punishment signal is associated with either the dot or 3D pin stimulus, smaller than an ommatidial pixel at this distance, delivered through an infrared laser. After training, without any heat punishment, the extent to which the fly has learned to avoid the tested stimulus is measured. Flies with normal binocular vision (above) exhibit significant learning scores, indicating their ability to see the dots and the pins as different objects. However, flies with monocular vision (one eye painted black, middle) or mutants that exhibit lateral photoreceptor microsaccades only in one eye (below) cannot learn this task. These results show that *Drosophila* has hyperacute stereovision (Kemppainen et al., 2022). Notably, this flight simulator-based setup did not allow simultaneous monitoring of photoreceptor microsaccades and whole-retina movements, both likely crucial to *Drosophila* stereovision and the observed visual behaviours. Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Video 2.

Behavioural experiments in a flight simulator verified that *Drosophila* possesses hyperacute stereovision (Kemppainen et al., 2022) (Fig. 5**C**). Tethered head-fixed flies were presented with 1-4° 3D and 2D objects, smaller than their eyes' average interommatidial angle (cf. Fig. 2**E**). Notably, the flies exhibited a preference for fixating on the minute 3D objects, providing support for the new morphodynamic sampling theory of hyperacute stereovision.

In subsequent learning experiments, the flies underwent training to avoid specific stimuli, successfully showing the ability to discriminate between small (≪ 4°) equal-contrast 3D and 2D objects. Interestingly, because of their immobilised heads, flies could not rely on motion parallax signals during learning, meaning the discrimination relied solely on the eyes' image disparity signals. Flies with one eye painted over failed to learn the stimuli. Moreover, it was discovered that rescuing R1-6 or R7/R8 photoreceptors in blind $norpA^{P24}$ mutants made their microsaccades' lateral (sideways) component more vulnerable to mechanical stress or developmental issues, with ~10 % of these mutants displaying microsaccades only monocularly(Kemppainen et al., 2022). However, both eyes showed a characteristic electroretinogram response, indicating intact phototransduction and axial microsaccade movement. Flies with normal lateral microsaccades learned to distinguish hyperacute 3D pins from 2D dots and the standard 2D T vs. ⊥ patterns, though less effectively than wild-type flies, showing that R1-6 input suffices for hyperacute stereovision but that R7/R8s also play a role. Conversely, mutants with monocular sideways microsaccades failed to learn 3D objects or 2D patterns, indicating that misaligned binocular sampling impairs 3D perception and learning. R7/R8 rescued $norpA^{P24}$ and $ninaE^{8}$ mutants confirmed that inner photoreceptors contribute to hyperacute stereopsis.

These results firmly establish the significance of binocular mirror-symmetric photoreceptor microsaccades in sampling 3D information and that both R1-6 (associated with motion vision (Borst, 2009) and R7/R8 (associated with colour vision (Song and Lee, 2018) photoreceptor classes contribute to hyperacute stereopsis. The findings provide compelling evidence that mirror-symmetric microsaccadic sampling, as a form of ultrafast neural morphodynamics, is necessary for hyperacute stereovision in *Drosophila* (Kemppainen et al., 2022).

2.6. Microsaccade variability combats aliasing

The heterogeneous nature of the fly's retinal sampling matrix – characterised by varying rhabdomere sizes (Juusola et al., 2017), random distributions of visual pigments (Johnston and Desplan, 2010), variations in photoreceptor synapse numbers (Rivera-Alba et al., 2011) (Fig. 6**A**), the stochastic integration of single photon responses (Juusola and Hardie, 2001; Juusola and Hardie, 2001; Song et al., 2012) (quantum bumps) (Juusola and Song, 2017; Juusola et al., 2017; Song et al., 2021) and stochastic variability in microsaccade waveforms (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022) – eliminates spatiotemporal aliasing (Juusola et al., 2017; Kemppainen et al., 2022) (Fig. 6**B**), enabling reliable transmission of visual information. This reliable encoding from variable samples aligns with the earlier examples (Fig. 2**C-D, 3D and 5B**) and touches on Francis Galton's idea of *vox populi* (Galton, 1907): "The mean of variable samples, reported independently by honest observers, provides the best estimate of the witnessed event" (Juusola et al., 2022). Consequently, the morphodynamic information sampling theory (Juusola et al., 2017; Kemppainen et al., 2022) challenges previous assumptions of *static* compound eyes (Land, 1997), which suggested that the ommatidial grid of immobile photoreceptors structurally limits spatial resolution, rendering the eyes susceptible to undersampling the visual world and prone to aliasing (Land, 1997).

Supporting the morphodynamic theory (Juusola et al., 2017;

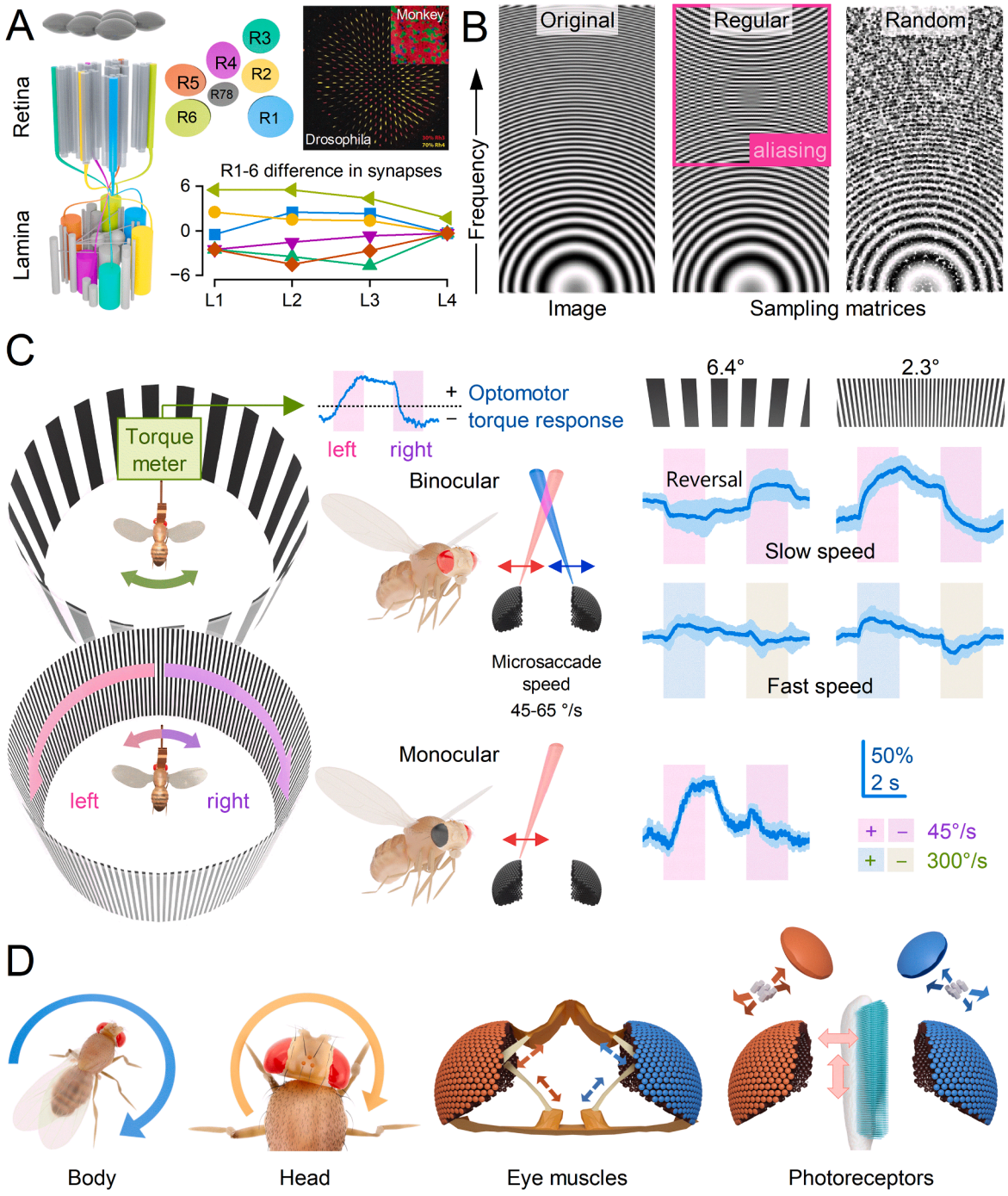


Fig. 6. Stochasticity and variations in the ommatidial photoreceptor grid structure and function combat spatiotemporal aliasing in morphodynamic information sampling and processing. (A) *Drosophila* R1-R7/8 photoreceptors are differently sized and asymmetrically positioned (Juusola et al., 2017; Kemppainen et al., 2022), forming different numbers of synapses with interneurons (Rivera-Alba et al., 2011) (L1-L4). Moreover, R7y and R7p receptors' colour sensitivity (Vasiliauskas et al., 2011) establishes a random-like sampling matrix, consistent with anti-aliasing sampling (Dippé and Wold, 1985; Juusola et al., 2017). The inset shows similar randomisation for the macaque retina(Field et al., 2010) (red, green and blue cones) (B) Demonstration of how a random sampling matrix eliminates aliasing (Juusola et al., 2017). An original $\sin(x^2 + y^2)$ image in 0.1 resolution. Under-sampling this image with 0.2 resolution by a regular sampling matrix leads to aliasing: ghost rings appear (pink square), which the nervous system cannot differentiate from the original real image. Sampling the original image with a 0.2 resolution random matrix loses some of its fine resolution due to broadband noise, but sampling is aliasing-free. (C) In the flight simulator optomotor paradigm, a tethered head-fixed *Drosophila* robustly responds to hyperacute stimuli (tested from ~ 0.5° to ~ 4° wavelengths) for different velocities (tested from 30°/s to 500°/s). However, flies show a response reversal to 45°/s rotating 6.4°-stripe panorama. In contrast, monocular flies, with one eye painted black, do not reverse their optomotor responses, indicating that the reversal response is not induced by spatial aliasing (Kemppainen et al., 2022). Notably, this flight simulator-based setup did not allow for the simultaneous monitoring of photoreceptor microsaccades and whole-retina movements, both of which must contribute to the flies' optomotor behaviour. (D) The compound eyes' active stereo information sampling integrates body, head movements and global retina movements with local photomechanical photoreceptor microsaccades. Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

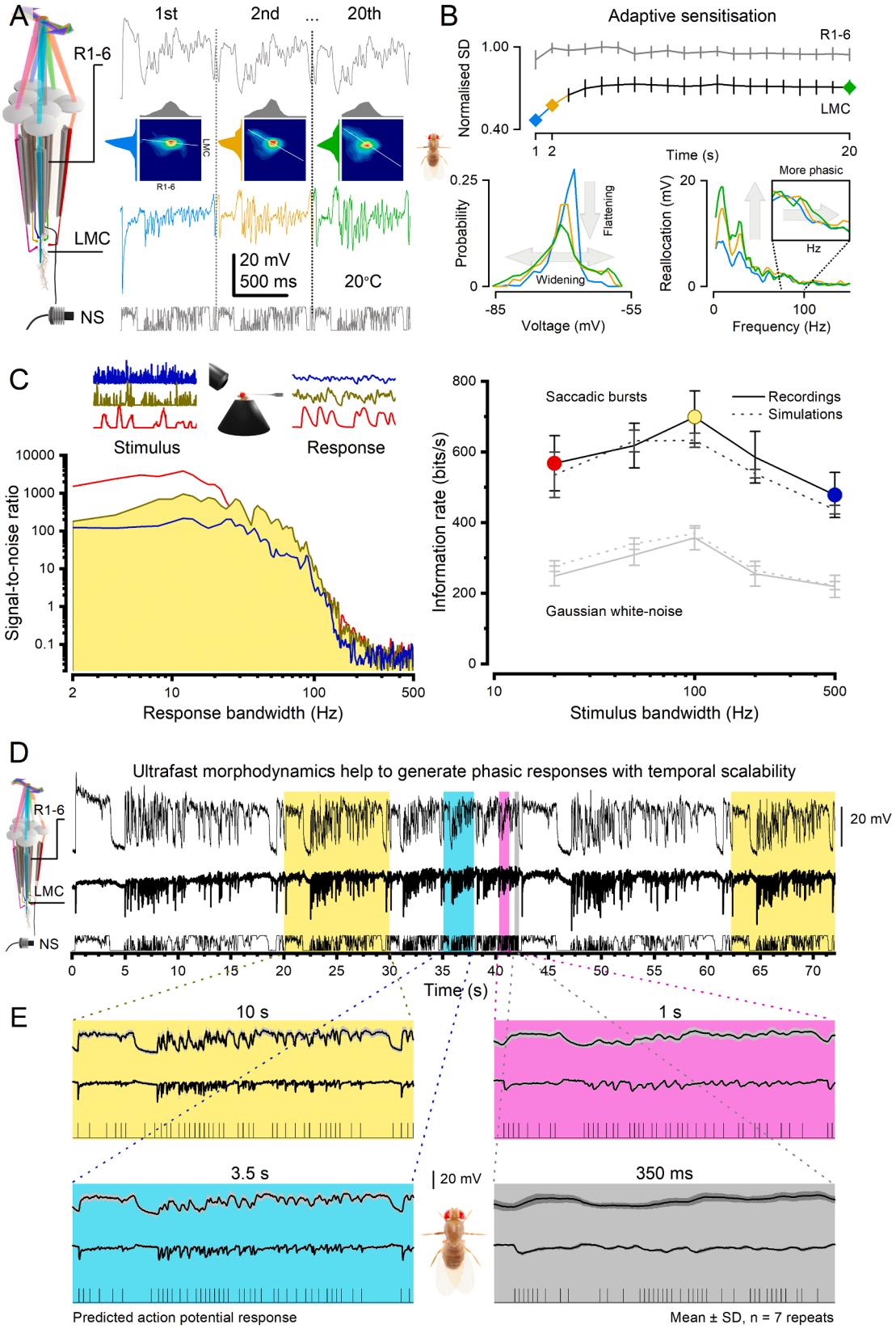


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Fig. 7. Pre- and postsynaptic morphodynamic sampling adapt to optimise information allocation in neural channels. (A) Adaptation enhances sensory information flow over time. R1–6 photoreceptor (above) and LMC voltage responses (below), as recorded intracellularly from *Drosophila* compound eyes in vivo, to a repeated naturalistic stimulus pattern, NS^{45}. The recordings show how these neurons' information allocation changes over time (for 1st, 2nd and 20th s of stimulation). The LMC voltage modulation grows rapidly over time, whereas the photoreceptor output changes less, indicating that most adaptation in the phototransduction occurs within the first second. Between these traces are their probability and the joint probability density functions ("hot" colours denote high probability). Notably, the mean synaptic gain increases dynamically as presented by the shape of join probability; white lines highlight its steepening slope during repetitive NS^{45} . (B) LMC output sensitises dynamically (Zheng et al., 2009): its probability density flattens and widens over time (arrows; from blue to green), causing a time-dependent upwards trend in standard deviation (SD). Simultaneously, its frequency distribution changes. Because both its low- (up arrow) and high-frequency (up right) content increases while R1-6 output is less affected, the synapse allocates information more evenly within the LMC bandwidth over time. (C) Left: Signal-to-noise ratio (SNR) of *Drosophila* R1-6 photoreceptor responses to 20 Hz (red), 100 Hz (yellow), and 500 Hz (blue) saccade-like contrast bursts (Juusola et al., 2017). SNR increases with contrast (right) and reaches its maximum value (~6,000) for 20 Hz bursts (red, left), while 100 Hz bursts (yellow) exhibit the broadest frequency range. Right: Information transfer rate comparisons between photoreceptor recordings and stochastic model simulations for saccadic light bursts and Gaussian white noise stimuli of varying bandwidths (Juusola et al., 2017). The estimated information rates from both recorded and simulated data closely correspond across the entire range of encoding tested. This indicates that the morphodynamic refractory sampling (as performed by 30,000 microvilli) generates the most information-rich responses to saccadic burst stimulation. (D) Adaptation to repetitive naturalistic stimulation shows phasic scale-invariance to pattern speed. 10,000 points-long naturalistic stimulus sequence (NS) was presented and repeated at different playback velocities, lasting from 20 s (0.5 kHz) to 333 ms (30 kHz) (Zheng et al., 2009). The corresponding intracellular photoreceptor (top trace) and LMC (middle trace) voltage responses are shown. The coloured sections highlight stimulus-specific playback velocities used during continuous recording. (E) The time-normalised shapes of the photoreceptor (above) and LMC (below) responses depict similar aspects of the stimulus, regardless of the playback velocity used (ranging from 0.5 to 30 kHz) (Zheng et al., 2009). The changes in the naturalistic stimulus speed, which follow the time-scale invariance of 1/f statistics, maintain the power within the frequency range of LMC responses relatively consistent. Consequently, LMCs can integrate similar size responses (contrast constancy) for the same stimulus pattern, irrespective of its speed (Zheng et al., 2009). These responses are predicted to drive generation of self-similar (scalable) action potential representations of the visual stimuli in central neurons. Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Kemppainen et al., 2022), tethered head-fixed *Drosophila* exhibit robust optomotor behaviour in a flight simulator system (Fig. 6**C**). The flies generated yaw torque responses, represented by the blue traces, indicating their intention to follow the left or right turns of the stripe panorama. These responses are believed to be a manifestation of an innate visuomotor reflex aimed at minimising retinal image slippage (Götz, 1968; Land, 1997). Consistent with *Drosophila*'s hyperacute ability to differentiate small 3D and 2D objects (Kemppainen et al., 2022), as shown earlier in Fig. 5**C**, the tested flies reliably responded to rotating panoramic black-and-white stripe scenes with hyperacute resolution, tested down to 0.5° resolution (Juusola et al., 2017; Kemppainen et al., 2022). This resolution is about ten times finer than the eyes' average interommatidial angle (cf. Fig. 2**E**), significantly surpassing the explanatory power of the traditional *static* compound eye theory (Land, 1997), which predicts 4°-5° maximum resolvability.

However, when exposed to slowly rotating 6.4-10° black-and-white stripe waveforms, a head-fixed tethered *Drosophila* displays reversals in its optomotor flight behaviour (Kemppainen et al., 2022) (Fig. 6**C**). Previously, this optomotor reversal was thought to result from the static ommatidial grid spatially aliasing the sampled panoramic stripe pattern due to the stimulus wavelength being approximately twice the eyes' average interommatidial angle. Upon further analysis, the previous interpretation of these reversals as a sign of aliasing (Fenk et al., 2022; Land, 1997) is contested. Optomotor reversals primarily occur at 40-60°/s stimulus velocities, matching the speed of the left and right eyes' mirror-symmetric photoreceptor microsaccades (Kemppainen et al., 2022) (Fig. 6**C**; cf. Fig. 2**C**). As a result, one eye's moving photoreceptors are more likely to be locked onto the rotating scene than those in the other eye, which move against the stimulus rotation. This discrepancy creates an imbalance that the fly's brain may interpret as the stimulus rotating in the opposite direction (Kemppainen et al., 2022).

Notably, the optomotor behaviour returns to normal when the tested fly has monocular vision (with one eye covered) and during faster rotations (Kemppainen et al., 2022) or finer stripe pattern waveforms (Juusola et al., 2017; Kemppainen et al., 2022) (Fig. 6**C**). Therefore, the abnormal optomotor reversal, which arises under somewhat abnormal and specific stimulus conditions when tested with head-fixed and position-constrained flies, must reflect high-order processing of binocular information and cannot be attributed to spatial sampling aliasing that is velocity and left-vs-right eye independent (Kemppainen et al., 2022).

2.7. Multiple layers of active sampling vs simple motion detection models

In addition to photoreceptor microsaccades, insects possess intraocular muscles capable of orchestrating coordinated oscillations of the entire photoreceptor array, encompassing the entire retina (Fenk et al., 2022; Hengstenberg, 1971; Juusola et al., 2017; Kemppainen et al., 2022) (Fig. 6**D**). This global motion has been proposed as a means to achieve hyperacuity (Colonnier et al., 2015; Viollet et al., 2014), but not for stereopsis. While the muscle movements alter the light patterns reaching the eyes, leading to the occurrence of photoreceptor microsaccades, it is the combination of local microsaccades and global retina movements, which include any body and head movements (Boeddeker et al., 2010; Schilstra and Van Hateren, 1999; Talley et al., 2023; van Hateren and Schilstra, 1999) (Fig. 6**D**), that collectively govern the active sampling of stereoscopic information by the eyes (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022).

The *Drosophila* brain effectively integrates depth and motion computations using mirror-symmetrically moving image disparity signals from its binocular vision channels (Kemppainen et al., 2022). During goal-oriented visual behaviours, coordinated muscle-induced vergence movements of the left and right retinae(Fenk et al., 2022), a phenomenon also observed in larger flies walking on a trackball (Franceschini and Taddei-Ferretti, 1998; Franceschini et al., 1995), likely further extend the stereo range by drawing bordering photoreceptors into the eye's binocular region (cf. **Text Box 1B iv**). Interestingly, in fully immobilised *Drosophila*, which rarely shows these retinal movements (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022), the photoreceptor microsaccade amplitudes characteristically fluctuate more during repeated light stimuli than the corresponding intracellular voltage responses (Juusola et al., 2017; Kemppainen et al., 2022). This suggests that, in addition to retinal movements, the fly brain might exert top-down control over retinal muscle tone and tension, thereby modulating the lateral range of photomechanical microsaccades through retinal strain adjustments. This interaction between retinal muscles and photoreceptor microsaccades could ultimately facilitate attentive accommodation, allowing the fly to precisely focus its hyperacute gaze on specific visual targets, analogous to how vertebrate lens eyes use ciliary muscles to fine-tune focus (Glasser and Dartt, 2010).

Conversely, by maximally tensing or relaxing the retinal muscles – and thus the retinae – a fly might be able to fully suppress the microsaccades' lateral movement, as suggested by studies involving optogenetic activation or genetic inactivation of retinal motor neurons (Fenk

et al., 2022). While photomechanical microsaccades are robust and occur without muscle involvement, as observed in dissociated photoreceptors in a Petri dish (Juusola et al., 2017), their lateral movement range can be physically constrained by increasing the stiffness of the surrounding medium. For example, in *spam*-mutant eyes, where the open rhabdom of R1-8 photoreceptors reverts to an ancestral fused rhabdom state (Osorio, 2007; Zelhof et al., 2006); microsaccade kinematics are similar to those in wild-type photoreceptors, but their

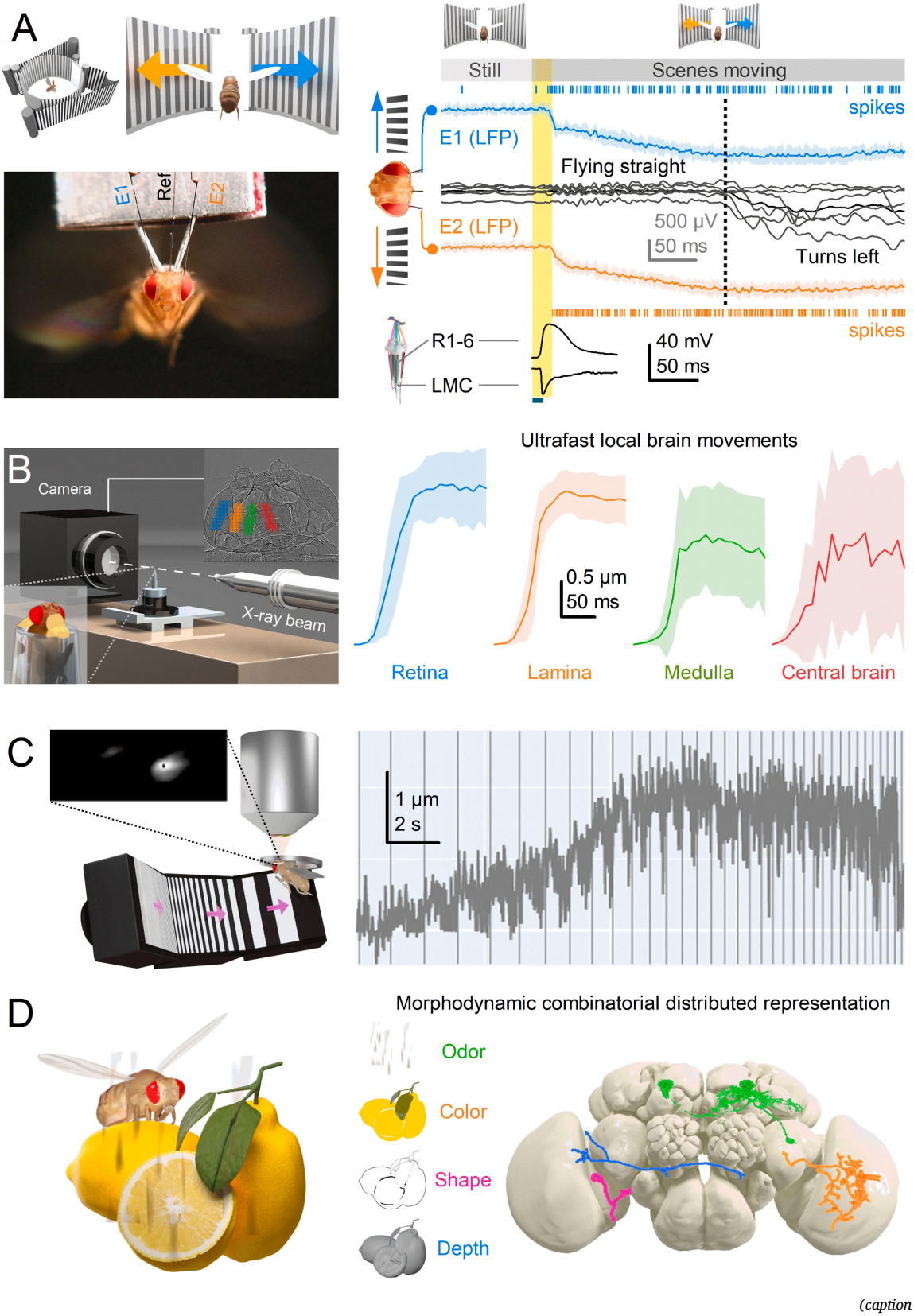

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Fig. 8. Synchronised minimal delay brain activity. (A) A *Drosophila* has three electrodes inserted into its brain: right (E1) and left (E2) lobula/lobula plate optic lobes and reference (Ref). It flies in a flight simulator seeing identical scenes of black and white stripes on its left and right (Tang and Juusola, 2010). When the scenes are still, the fly flies straight, and the right and left optic lobes show little activity; only a sporadic spike and the local field potentials (LFPs) are flat (E2, blue; E1, red traces). When the scenes start to sweep to the opposing directions, it takes less than 20 ms (yellow bar) for the optic lobes to respond to these visual stimuli (first spikes, and dips in LFPs). Interestingly, separate intracellular photoreceptor and large monopolar cell (LMC) recordings to 10 ms light pulse shows comparable time delays, peaking on average at 15 ms and 10 ms, respectively. Given that lobula and lobula plate neurons, which generate the observed spike and LFP patterns, are at least three synapses away from photoreceptors, the neural responses at different processing layers (retina, lamina, lobula plate) are closely synchronised, indicating minimal delays. Even though the fly brain has already received the visual information about the moving scenes, the fly makes little adjustments in its flight path, and the yaw torque remains flat. Only after minimum of 210 ms of stimulation, the fly finally chooses the left stimulus by attempting to turn left (dotted line), seen as intensifying yaw torque (downward). (B) Brief high-intensity X-ray pulses activate *Drosophila* photoreceptors (Kemppainen et al., 2022), causing photomechanical photoreceptor microsaccades across the eyes (characteristic retina movement). Virtually simultaneously, also other parts of the brain move, shown for Lamina, Medulla and Central brain. (C) During 2-photon imaging, L2-monopolar cell terminals can show mechanical jitter (grey noisy trace) that is synchronised with moving stimulus (Kemppainen et al., 2022) (vertical stripes). (D) *Drosophila* brain networks likely utilise multiple synchronised morphodynamic neural pathways to integrate a continuously adjusted, combinatorial, and distributed neural representation of a lemon, leading to its coherent and distinct object perception. Data are modified from the cited papers to illustrate the main effects in an intuitive manner. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

displacement range is reduced due to the increased structural stiffness of the fused rhabdom (Kemppainen et al., 2022). If the maximally tensing or relaxing of the retinal muscles were linked to top-down synaptic inhibition of photoreceptor signals – potentially mediated by centrifugal GABAergic C2/C3 fibres (Kolodziejczyk et al., 2008) from the brain that innervate the photoreceptors (Rivera-Alba et al., 2011) – this centralised visual information suppression ("closing the eyes") could serve to minimise environmental interference and the eyes' energy consumption during sleep.

These findings and new ideas about fast and complex motion-based interactions in visual information sampling and processing challenge the traditional view that insect brains rely on low-resolution input from static eyes for high-order computations. For instance, the motion detection ideals of reduced input–output systems (Borst, 2009; de Polavieja, 2006; Yang and Clandinin, 2018), such as Hassenstein-Reichardt (Hassenstein and Reichardt, 1956) and Barlow-Levick (Barlow and Levick, 1965) models, require updates to incorporate ultrafast morphodynamics (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022), retinal muscle movements (Fenk et al., 2022) and state-dependent synaptic processing (Chiappe et al., 2010; Grabowska et al., 2020; Leung et al., 2021; Maimon et al., 2010; Tang and Juusola, 2010). The updates are crucial as these processes actively shape neural responses, perception, and behaviours (Tang and Juusola, 2010), providing essential ingredients for hyperacute attentive 3D vision (Juusola et al., 2017; Kacsoh et al., 2013; Kemppainen et al., 2022; Sheehan and Tibbetts, 2011) and intrinsic decision-making (Juusola et al., 2017; Kemppainen et al., 2022; Maye et al., 2007; van Hateren, 2017; van Hateren, 2019) that occur in a closed-loop interaction with the changing environment.

Accumulating evidence, consistent with the idea that brains reduce uncertainty by synchronously integrating multisensory information (Okray et al., 2023), further suggests that object colour and shape information partially streams through the same channels previously thought to be solely for motion information (Wardill et al., 2012). Consequently, individual neurons within these channels should engage in multiple parallel processing tasks (Wardill et al., 2012), adapting in a phasic and goal-oriented manner. These emerging concepts challenge oversimplified input–output models of insect vision, highlighting the importance of complex interactions between local ultrafast neural morphodynamics and global active vision strategies in perception and behaviour.

3. Benefits of neural morphodynamics

Organisms have adapted to the quantal nature of the dynamic physical world, resulting in ubiquitous active use of quantal morphodynamic processes and signalling within their constituent parts, as we highlighted in Fig. 1 in the Introduction. Besides enhancing information sampling and flow in sensory systems for efficient perception (Bocchero et al., 2020; Hardie and Franze, 2012; Hudspeth, 2008; Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022; Pandiyan et al., 2020; Senthilan et al., 2012), we propose that ultrafast neural morphodynamics likely evolved universally to facilitate effective communication across nervous systems (Crick, 1982; Korkotian and Segal, 2001; Majewska and Sur, 2003; Watanabe et al., 2013). By aligning with the moving world principles of thermodynamics and information theory (de Polavieja, 2002; de Polavieja, 2004; Juusola and de Polavieja, 2003), the evolution of nervous systems harnesses neural morphodynamics to optimise perception and behavioural capabilities, ensuring efficient adaptation to the ever-changing environment. The benefits of ultrafast morphodynamic neural processing are substantial and encompass the following:

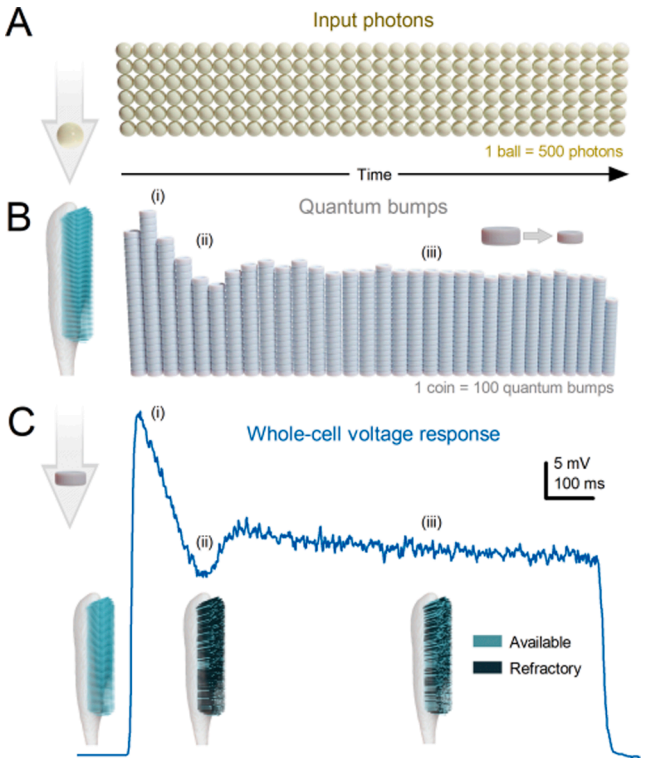
3.1. *Efficient neural encoding of reliable representations across wide dynamic range*

Neural communication through synapses relies on rapid pre- and postsynaptic ultrastructural movements (Joy et al., 2023) that facilitate efficient quantal release and capture of neurotransmitter molecules (Juusola et al., 1995; Juusola et al., 1996; Watanabe et al., 2013). These processes share similarities with how photoreceptor microvilli have evolved to utilise photomechanical movements (Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022) with quantal refractory photon sampling (Juusola and Song, 2017; Juusola et al., 2017; Song et al., 2012) to maximise information in neural responses (e.g. Fig. 3**D**). In both systems, ultrafast morphodynamics are employed with refractoriness to achieve highly accurate sampling of behaviourally or intrinsically relevant information by rapidly adapting their quantum efficiency to the influx of vastly varying sample (photon vs neurotransmitter molecule) rate changes (Juusola and Song, 2017; Juusola et al., 2017; Kemppainen et al., 2022; Song et al., 2012).

In synaptic transmission (e.g. Fig. 1**D, E**), presynaptic transmitter vesicles are actively transported to docking sites by molecular motors (Rusakov et al., 2011). Within these sites, vesicle depletion occurs through ultrafast exocytosis, followed by replenishment via endocytosis (Watanabe et al., 2013). These processes generate ultrastructural movements, vesicle queuing and refractory pauses (Rusakov et al., 2011). Such movements and pauses occur as vesicle numbers, and potentially their sizes (Juusola et al., 1995), adapt to sensory or neural information flow changes. Given that a spherical vesicle contains many neurotransmitter molecules with a high rate of release, the transmitter molecules, acting as carriers of information, can exhibit logarithmic changes from one moment to another. Conversely, the adaptive morphodynamic processes at the postsynaptic sites involve rapid movements of dendritic spines (Majewska and Sur, 2003) (cf. Fig. 1**C**) or transmitter-receptor complexes (Rusakov et al., 2011) (e.g. Fig. 1**E**). These ultrastructural movements likely facilitate efficient sampling of information from the rapid changes in neurotransmitter concentration,

Box 2

Visualising Refractory Quantal Computations. By utilising powerful multi-scale morphodynamic neural models (Juusola et al., 2017; Kemppainen et al., 2022; Song et al., 2012), we can predict and analyse the generation and integration of voltage responses during morphodynamic quantal refractory sampling and compare these simulations to actual intracellular recordings for similar stimulation (Juusola et al., 2017; Kemppainen et al., 2022; Song et al., 2012). This approach, combined with information-theoretical analyses (Juusola and de Polavieja, 2003; Juusola and Hardie, 2001; Song and Juusola, 2014; Song et al., 2012), allows us to explain how phasic response waveforms arise from ultrafast movements and estimate the signal-to-noise ratio and information transfer rate of the neural responses. Importantly, these methods are applicable for studying the morphodynamic functions of any neural circuit. To illustrate the analytic power of this approach, we present a simple example: an intracellular recording (whole-cell voltage response) of dark-adapted *Drosophila* photoreceptors (**C**) to a bright light pulse. See also Fig. 2**D** which shows morphodynamic simulations of how a photoreceptor responds to two dots crossing its receptive field from east to west and west to east directions.



An insect photoreceptor's sampling units – e.g., 30,000 microvilli in a fruit fly or 90,000 in a blowfly R1-6 – count photons as variable samples (quantum bumps) and sum these up into a macroscopic voltage response, generating a reliable estimate of the encountered light stimulus. For clarity, visualise the light pulse as a consistent flow of photons, or golden balls, over time (**A**). The quantum bumps that the photons elicit in individual microvilli can be thought of as silver coins of various sizes (**B**). The photoreceptor persistently counts these "coins" produced by its microvilli, thus generating a dynamically changing macroscopic response (**C**, depicted as a blue trace). These basic counting rules (Juusola et al., 2022) shape the photoreceptor response:

- Each microvillus can produce only one quantum bump at a time (Hochstrate and Hamdorf, 1990; Howard et al., 1987; Pumir et al., 2008; Song et al., 2012).
- After producing a quantum bump, a microvillus becomes refractory for up to 300 ms (in *Drosophila* R1-6 photoreceptors at 25°C) and cannot respond to other photons (Hochstrate and Hamdorf, 1990; Mishra et al., 2007; Scott et al., 1997).
- Quantum bumps from all microvilli sum up the macroscopic response (Hochstrate and Hamdorf, 1990; Howard et al., 1987; Liu et al., 2008; Pumir et al., 2008; Song et al., 2012).
- Microvilli availability sets a photoreceptor's maximum sample rate (quantum bump production rate), adapting its macroscopic response to a light stimulus (Howard et al., 1987; Song et al., 2012).
- Global Ca^{2+} accumulation and membrane voltage affect samples of all microvilli. These global feedbacks strengthen with brightening light to reduce the size and duration of quantum bumps, adapting the macroscopic response (Juusola and Hardie, 2001; Juusola and Hardie, 2001; Juusola and Weckstrom, 1993; Juusola et al., 1994; Juusola, 1993; Wong and Knight, 1980; Wong et al., 1980).

Adaptation in macroscopic response (**C**) to continuous light (**A**) is mostly caused by a reduction in the number and size of quantum bumps over time (**B**). When the stimulus starts, a large portion of the microvilli is simultaneously activated (**A i** and **B i**), but they subsequently enter a refractory state (**A ii** and **B ii**). This means that a smaller fraction of microvilli can respond to the following photons in the stimulus until more microvilli become available again. As a result, the number of activated microvilli initially peaks and then rapidly declines, eventually settling into a steady state (**A iii** and **B iii**) as the balance between photon arrivals and refractory periods is achieved. If all quantum bumps were identical, the macroscopic current would simply reflect the number of activated microvilli based on the photon rate, resulting in a steady-state response. Light-induced current also exhibits a decaying trend towards lower plateau levels. This is because quantum bumps adapt to brighter backgrounds (**A iii** and **B iii**), becoming smaller and briefer (Juusola and Hardie, 2001; Juusola and Hardie, 2001). This adaptation is caused by

global negative feedback, Ca^{2+}-dependent inhibition of microvillar phototransduction reactions (Hardie et al., 2008; Hardie, 1996; Postma et al., 1999; Wong and Knight, 1980; Wong et al., 1980). Additionally, the concurrent increase in membrane voltage compresses responses by reducing the electromotive force for the light-induced current across all microvilli (Song et al., 2012). Together, these adaptive dynamics enhance phasic photoreceptor responses, similar to encoding phase congruency (Friederich et al., 2016).

The signal-to-noise ratio and rate of information transfer increase with the average sampling rate, which is the average number of samples per unit time. Thus, the more samples that make up (integrate) the macroscopic response to a given light pattern, the higher its information transfer rate. However, with more photons being counted by a photoreceptor at brightening stimulation, information about saccadic light patterns of natural scenes in its responses first increases and then approaches a constant rate. This is because:

(a) When more microvilli are in a refractory state, more photons fail to generate quantum bumps. As quantum efficiency drops, the equilibrium between used and available microvilli approaches a constant (maximum) quantum bump production rate (sample rate). This process effectively performs division, scaling logarithmic changes in photon rates into macroscopic voltage responses with consistent size and waveforms, thereby maintaining contrast constancy (Juusola et al., 2022; Song and Juusola, 2014; Song et al., 2012).

(b) Once global Ca^{2+} and voltage feedbacks saturate, they cannot make quantum bumps any smaller and briefer with increasing brightness.

(c) After initial acceleration from the dark-adapted state, quantum bump latency distribution remains practically invariable in different light-adaptation states (Juusola and Hardie, 2001).

Therefore, when sample rate modulation (a) and sample integration dynamics (b and c) of the macroscopic voltage responses settle (at intensities $>10^5$ photons/s in *Drosophila* R1-6 photoreceptors, allocation of visual information in the photoreceptor's amplitude and frequency range becomes nearly invariable (Song et al., 2012; Song and Juusola, 2014; Faivre and Juusola, 2008). Correspondingly, stochastic simulation closely predicts measured responses and rates of information transfer (Juusola and Song, 2017; Song and Juusola, 2014; Song et al., 2012). Notably, when the microvilli usage reaches a midpoint (~50 % level), the information rate encoded by the macroscopic responses to natural light intensity time series saturates (Song et al., 2012). This is presumably because sample rate modulation to light increments and decrements – which in the macroscopic response code for the number of different stimulus patterns (Juusola and de Polavieja, 2003) – saturate. Quantum bump size, if invariable, does not affect the information transfer rate – as long as the quantum bumps are briefer than the stimulus changes they encode. Thus, like any other filter, a fixed bump waveform affects signal and noise equally (Data Processing theorem (Song et al., 2012; Juusola and de Polavieja, 2003). But varying quantum bump size adds noise; when this variation is adaptive (memory-based), less noise is added (Juusola and de Polavieja, 2003; Song et al., 2012).

In summary, insect photoreceptors count photons through microvilli, integrate the responses, and adapt their macroscopic response based on the basic counting rules and global feedback mechanisms. The information transfer rate increases with the average sampling rate but eventually reaches a constant rate as the brightness of the stimulus increases. The size of the quantum bumps affects noise levels, with adaptive variation reducing noise.

enabling swift and precise integration of macroscopic responses from the sampled postsynaptic quanta (Juusola et al., 1995; Juusola et al., 1996).

Interestingly, specific circuits have evolved to integrate synchronous high signal-to-noise information from multiple adjacent pathways, thereby enhancing the speed and accuracy of phasic signals (Juusola et al., 1995; Juusola et al., 1996; Li et al., 2019; Zheng et al., 2006; Zheng et al., 2009). This mechanism is particularly beneficial for computationally challenging tasks, such as distinguishing object boundaries from the background during variable self-motion. For instance, in the photoreceptor-LMC synapse (Fig. 7), the fly eye exhibits neural superposition wiring (Kirschfeld, 1973), allowing each LMC to simultaneously sample and integrate quantal events from six neighbouring photoreceptors (R1-6), driven by the morphodynamics detailed in Fig. 5**B** and Video 2. Because the receptive fields of these photoreceptors only partially overlap and move in slightly different directions during microsaccades, each photoreceptor conveys a distinct phasic aspect of the visual stimulus to the LMCs (Kemppainen et al., 2022) (L1-3; cf. Fig. 6**A** that illustrates their synaptic dispersion). The LMCs actively differentiate these inputs, resulting in rapidly occurring phasic responses with notably high signal-to-noise ratios, particularly at high frequencies (Juusola et al., 1995; Juusola et al., 1996; Zheng et al., 2006; Zheng et al., 2009).

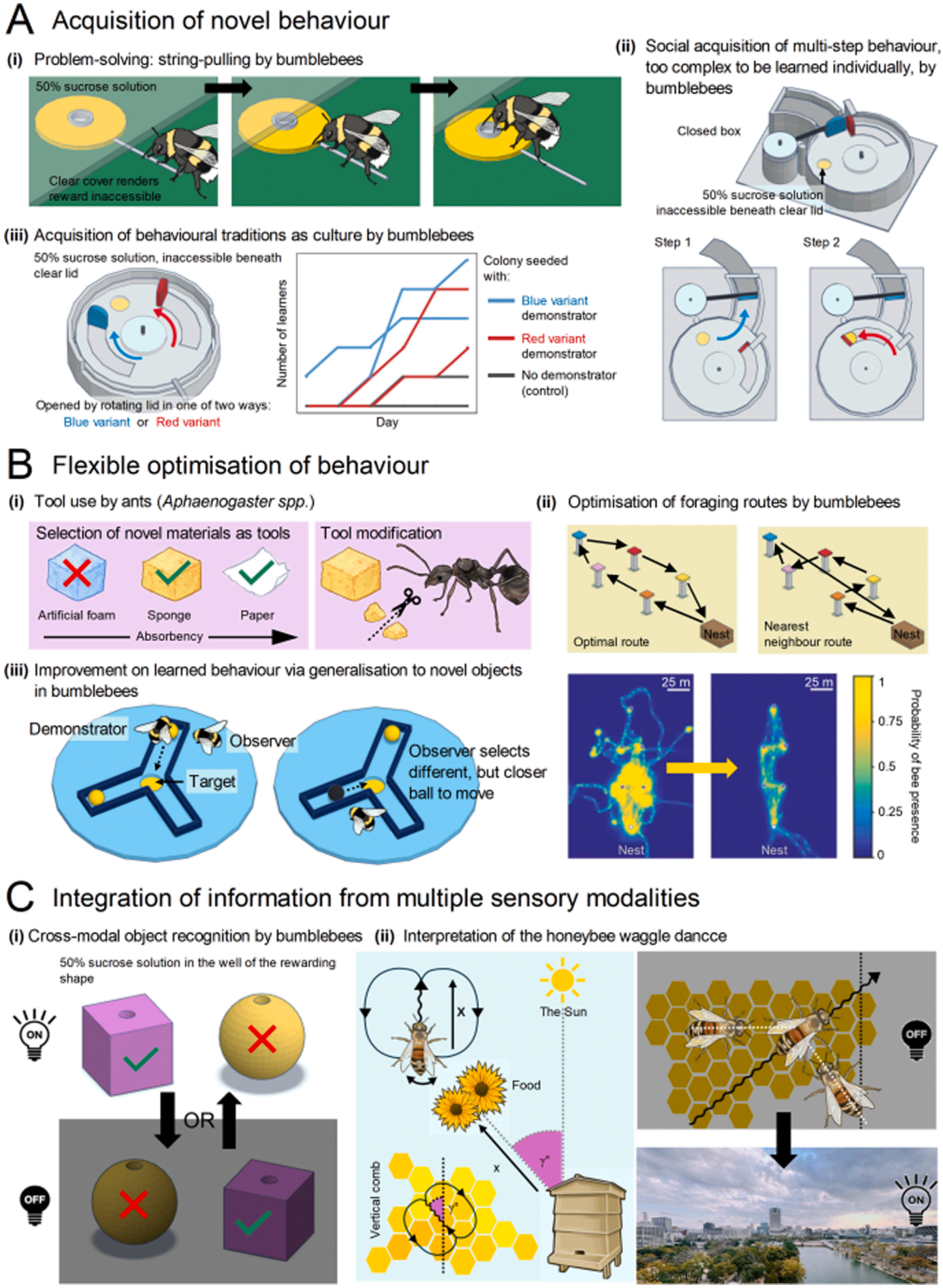
Moreover, in this system, coding efficiency improves dynamically by adaptation (Fig. 7**A**), which swiftly flattens and widens the LMC's amplitude and frequency distributions over time (Juusola et al., 1995; Juusola et al., 1996) (Fig. 7**B**), improving sensitivity to under-represented signals within seconds. Such performance implies that LMCs strive to utilise their output range equally in different situations since a message in which every symbol is transmitted equally often has the highest information content (Shannon, 1948). Here, an LMC's sensory information is maximised through pre- and postsynaptic morphodynamic processes, in which quantal refractory sampling jointly adapts to light stimulus changes, dynamically adjusting the synaptic gain (Fig. 7**A**; see the R-LMC joint probability at each second of stimulation, where the slope of the white line indicates the dynamic gain change).

Comparable to LMCs, dynamic adapting scaling for information maximisation has been shown in blowfly H1 neurons' action potential responses (spikes) to changing light stimulus velocities (Brenner et al., 2000). These neurons reside in the lobula plate optic lobe, deeper in the brain, at least three synapses away from LMCs. Therefore, it is possible that H1s' adaptive dynamics partly project the earlier morphodynamic quantal information sampling in the photoreceptor-LMC synapse or that adaptive rescaling is a general property of all neural systems (Arganda et al., 2007; Maravall et al., 2007). Nevertheless, the continuously adapting weighted-average of the six variable photoreceptor responses reported independently to LMCs, combat noise and may carry the best (most accurate unbiased) running estimate of the ongoing light contrast signals. This *dynamic* maximisation of sensory information is distinct from the well-known original concept of *static* contrast equalisation (Laughlin, 1981). The latter is based on stationary image statistics of a limited range and necessitates an implausible static synaptic encoder system (Zheng et al., 2009) that imposes a constant synaptic gain. Furthermore, this model does not address the quantal stochastic properties of neural processing (Song et al., 2012; Song et al., 2021; Zheng et al., 2009).

Thus, ultrafast morphodynamics actively shapes neurons' macroscopic voltage response waveforms maximising information flow. These adaptive dynamics impact both the presynaptic quantal transmitter release and postsynaptic integration of the sampled quanta, influencing the underlying quantum bump size, latency, and refractory distributions (Juusola et al., 2017). Advantageously, intracellular microelectrode recordings in vivo provide a means to estimate these distributions statistically with high accuracy (Juusola and Hardie, 2001; Juusola and Hardie, 2001; Juusola et al., 1995; Juusola et al., 1996). Knowing these distributions and the number of sampling units obtained from ultrastructural electron microscopy data, one can accurately predict neural

Box 3

Challenging Static Models of Insect Cognition. Insects, with their often short lifespans and miniature neural architectures, were once widely regarded as simple, reactive organisms, limited to executing pre-programmed responses to specific stimuli. This perspective aligned with simplified input–output models of perception based on static neural processing structures (Land, 1997; Laughlin, 1989; Stavenga, 2003). However, recent research has increasingly challenged these models, highlighting their shortcomings in accounting for the sophisticated cognitive abilities demonstrated by insects. (Each panel presents data adapted from the referenced studies.)



(A) Acquisition of Novel Behaviour. Insects can acquire new behaviours through multiple pathways, including individual trial-and-error learning and social learning from knowledgeable conspecifics. In these cases, neural morphodynamics – if universally employed by neural circuits –could play a crucial role in enabling the brain to adapt and reconfigure its local structures efficiently, optimising learning performance in response to changing environmental conditions and experiences.

The use of non-natural paradigms –situations that insects would not typically encounter in their natural environments – further emphasises the non-innate nature of these behaviours. Despite their unfamiliarity with the following tasks, insects demonstrated remarkable adaptability and learning capacities:

i. Bumblebees can learn to pull strings to obtain out-of-reach rewards, both through individual learning and social transmission (Alem et al., 2016).
ii. Bumblebees can socially learn a complex two-step behaviour that they cannot learn individually – previously thought to be a human-exclusive capability underlying our species' cumulative culture (Bridges et al., 2024).
iii. In laboratory settings, bumblebees can acquire local variations of novel behaviours as a form of culture, even though such behaviours are not observed in the wild (Bridges et al., 2023).

(B) Flexible Optimisation of Behaviour. In response to changing environmental demands, insects can successfully and flexibly optimise their behaviour to improve their fitness.

i. Ants (*Aphaenogaster* spp.) select and modify tools based on their soaking properties and the viscosity of food sources. They not only learn to use novel objects like sponges and paper as tools but also modify these objects by tearing them into smaller, more manageable pieces (Lorinczi et al., 2018; Maák et al., 2017).
ii. Bumblebees optimise their foraging routes between multiple locations, effectively solving the "travelling salesman problem" by reducing flight distance and duration with experience (Woodgate et al., 2017).
iii. Bumblebees can be trained to roll a ball to a marked location for a reward. After observing knowledgeable conspecifics, they not only learn this behaviour but also generalise it to novel balls, preferring the more efficient option even if this differed from the option used by their conspecifics (Loukola et al., 2017).

(C) Integration of Information Across Multiple Sensory Modalities The ability to recognise objects across different sensory modalities is inherently adaptive (Hadjitofi and Webb, 2024; Suver et al., 2023), leading to richer and more accurate environmental representations. This cognitive ability likely plays a role in the processes described in sections A and B.

i. Bumblebees (*Bombus terrestris*) can recognise three-dimensional objects, such as spheres and cubes, by touch if they have only seen them and by sight if they have only touched them (Solvi et al., 2020).
ii. Honeybees (*Apis mellifera*) can interpret the waggle dance of successful foragers in darkness by detecting the dancer's movements with their antennae. They then translate these movements into an accurate flight vector encoding distance and direction relative to the sun (Hadjitofi and Webb, 2024).

responses and their information content for any stimulus patterns (Juusola and de Polavieja, 2003; Juusola and Hardie, 2001; Juusola and Hardie, 2001; Juusola and Song, 2017; Juusola et al., 1996). These 4-parameter quantal sampling models, which avoid the need for free parameters (Juusola et al., 2017; Kemppainen et al., 2022; Song and Juusola, 2014; Song et al., 2012; Song et al., 2021), have been experimentally validated (Juusola and de Polavieja, 2003; Juusola and Hardie, 2001; Juusola and Hardie, 2001; Juusola et al., 1995; Juusola et al., 2017; Kemppainen et al., 2022; Song and Juusola, 2014; Song et al., 2012; Song et al., 2021) (Fig. 7**C**), providing a biophysically realistic multiscale framework to understand the involved neural computations (Juusola et al., 2017; Song et al., 2021).

From a computational standpoint, a neural sampling or transmission system exerts adaptive quantum efficiency regulation that can be likened to division (see **Text** Box 2). Proportional quantal sample counting is achieved through motion-enhanced refractory transmission, sampling units, or combinations. This refractory adaptive mechanism permits a broad dynamic range, facilitating response normalisation through adaptive scaling and integration of quantal information (Juusola and Song, 2017; Juusola et al., 2017; Kemppainen et al., 2022). Consequently, noise is minimised, leading to enhanced reliability of macroscopic responses (Juusola and Song, 2017; Juusola et al., 2017).

Therefore, we expect that this efficient information maximisation strategy, which has demonstrated signal-to-noise ratios reaching several thousand in insect photoreceptors during bright saccadic stimulation (Juusola and Song, 2017; Juusola et al., 2017) (Fig. 7**C**), will serve as a fundamental principle for neural computations involving the sampling of quantal bursts of information, such as neurotransmitter or odorant molecules. In this context, it is highly plausible that the pre- and postsynaptic morphodynamic quantal processes of neurons have co-adapted to convert logarithmic sample rate changes into precise phasic responses with limited amplitude and frequency distributions (Juusola et al., 1995; Juusola et al., 2017), similar to the performance seen in fly photoreceptor (Juusola and Hardie, 2001; Juusola and Hardie, 2001; Juusola et al., 2017; Kemppainen et al., 2022; Song et al., 2012) and first visual interneurons, LMCs (Juusola et al., 1995; Juusola et al., 1996). Hence, ultrafast refractory quantal morphodynamics may represent a prerequisite for efficiently allocating information within the biophysically constrained amplitude and frequency ranges of neurons (de Polavieja, 2004; Juusola and de Polavieja, 2003; van Hateren, 1992).

3.2. *Predictive coding and minimal neural delays*

Hopfield and Brody initially proposed that brain networks might employ transient synchrony as a collective mechanism for spatiotemporal integration for action potential communication (Hopfield and Brody, 2001). Interestingly, morphodynamic quantal refractory information sampling and processing may offer the means to achieve this general coding objective.

Neural circuits incorporate predictive coding mechanisms that leverage mechanical, electrical, and synaptic feedback to minimise delays (Juusola and Song, 2017; Juusola et al., 2017; Kemppainen et al., 2022). This processing, which enhances phasic inputs, synchronises the flow of information right from the first sampling stage (Juusola et al., 1995; Juusola et al., 2017; Zheng et al., 2009). It time-locks activity patterns into transient bursts of temporal scalability as observed in *Drosophila* photoreceptors' and LMCs' voltage responses to accelerating

naturalistic light patterns (Fig. 7**D, E**) (Hopfield and Brody, 2001; Juusola et al., 2017; Zheng et al., 2009). Such phasic synchronisation and scalability are crucial for the brain to efficiently recognise and represent the changing world, irrespective of the animal's self-motion, and predict and lock onto its moving patterns. As a result, perception becomes more accurate, and behavioural responses to dynamic stimuli are prompt.

Crucially, this adaptive scalability of phasic, graded potential responses is readily translatable to sequences of action potentials (Fig. 7**E**, cf. the scalable spike patterns predicted from the LMC responses). Thus, ultrafast neural morphodynamics may contribute to our brain's intrinsic ability to effortlessly capture the same meaning from a sentence, whether spoken very slowly or quickly. This dynamic form of predictive coding, which time-locks phasic neural responses to moving temporal patterns, differs markedly from the classic concept of interneurons using static centre-surround antagonism within their receptive fields to exploit spatial correlations in the natural scenes (Srinivasan et al., 1982).

Reinforcing the idea of fast morphodynamic synchronisation as a general phenomenon, we observe minimum phase responses deeper in the brain. In experiments involving tethered flying *Drosophila*, electrical activity patterns recorded from their lobula/lobula plate optic lobes (Tang and Juusola, 2010) – located at least three synapses downstream from photoreceptors – exhibit remarkably similar minimal delay responses to those seen in LMCs (Fig. 8**A**). These first responses emerge well within 20 ms of the stimulus onset (Tang and Juusola, 2010). Such rapid signal transmission through multiple neurons and synapses challenges traditional models that rely on the stationary eye and brain circuits with significant synaptic (chemical), signal integration and conduction (electrical) delays.

Thus, neural processing in vivo appears more synchronised and holistic, with signals being processed in a more integrated manner across different parts of the brain. This is also reflected by the brain's broadly distributed dynamic energy usage during activity (Mann et al., 2021). Instead of neurons conveying information sequentially like falling dominos, neural morphodynamics and multidirectional tonic synaptic operations connect the "neural dominos" with interlinked "strings" (push and pull mechanisms), causing them to fall together. This synchronised minimal-delay information processing across the brain – from sensing to decision-making – is likely a prerequisite for complex behaviours in real time.

Moreover, in vivo high-speed X-ray imaging (Kemppainen et al., 2022) has revealed synchronised phasic movements across the *Drosophila* optic lobes following the rapid microsaccades of light-activated photoreceptors (Fig. 8**B**). Synchronised tissue movements have also been observed during 2-photon imaging of optic lobe neurons (Kemppainen et al., 2022) (Fig. 8**C**). In the past, such movements have been often thought to be motion artefacts, with researchers making considerable efforts to eliminate them from calcium imaging data collection.

The absence of phasic amplification and synchronisation of signals through morphodynamics would have detrimental effects on communication speed and accuracy, resulting in slower perception and behavioural responses. It would significantly prolong the time it takes for visual information from the eyes to reach decision-making circuits, increasing uncertainty and leading to a decline in overall fitness. Thus, we expect the inherent scalability of neural morphodynamic responses (as demonstrated in Fig. 7**D**) to be crucial in facilitating efficient communication and synchronisation among different brain regions, enabling the coordination required for complex cognitive processes.

We propose that neurons exhibit morphodynamic jitter (stochastic oscillations) at the ultrastructural level sensitising the transmission system to achieve these concerted efforts. By enhancing phasic sampling, such jitter could minimise delays across the whole network, enabling interconnected circuits to respond in –sync to changes in information flow, actively co-differentiating the relevant (or attended) message stream (Tang and Juusola, 2010). Similarly, jitter-enhanced synchronisation could involve linking sensory (bottom-up) information about a moving object with the prediction (efference copy (Poulet and Hedwig, 2006; Poulet and Hedwig, 2007) of movement-producing signals generated by the motor system, or top-down prediction of the respective self-motion (Fujiwara et al., 2017). Their difference signal, or prediction error, could then be used to rectify the animal's self-motion more swiftly than without the jitter-induced delay minimisation and synchronous phase enhancement, enabling faster behavioural responses.

Historically, there has been significant interest in understanding how field potentials – transient electrical signals generated in neurons and surrounding cells through collective activity – convey or reflect synchronous brain activity, especially as frequency bands vary with an animal's activity state (Gallego-Carracedo et al., 2022; Peyrache et al., 2012; Yap et al., 2017). Specific low-frequency bands characterise different stages of sleep (Yap et al., 2017) – ranging from Delta (0.5–4 Hz) to Beta (13–30 Hz) – while Gamma-frequency activity (30–150 Hz) is consistently observed during selective attention across species from insects (Grabowska et al., 2020; Tang and Juusola, 2010; van Swinderen, 2011) to humans. Recently, cytoelectric coupling (Miller et al., 2024; Pinotsis et al., 2023) has been proposed to explain these phenomena. Regardless of the exact mechanisms, it is plausible that neural morphodynamics closely participates in this network activity or plays a synergistic role.

We also expect ultrafast morphodynamics to contribute to multisensory integration by temporally aligning inputs from diverse sensory modalities with intrinsic goal-oriented processing (Fig. 8**D**). This cross-modal synchronisation enhances behavioural certainty (Okray et al., 2023; Solvi et al., 2020). Using synchronised phasic information, a brain network can efficiently integrate yellow colour, shuttle-like shape, rough texture, and sweet scent into a unique neural representation, effectively identifying a *lemon* amidst the clutter and planning an appropriate action. These ultrafast combinatorial and distributed spatiotemporal responses expand the brain's capacity to encode information, increasing its representational dimensionality (Badre et al., 2021) beyond what could be achieved through slower processing in static circuits. Thus, the phasic nature of neural morphodynamics may enable animals to think and behave faster and more flexibly.

3.3. *Anti-aliasing and robust communication*

Neural morphodynamics incorporates anti-aliasing sampling and signalling mechanisms within the peripheral nervous system (Juusola et al., 2017; Kemppainen et al., 2022; Yellott, 1982) to prevent the distortion of sensory information. Like *Drosophila* compound eyes, photoreceptors in the primate retina exhibit varying sizes (Wikler and Rakic, 1990), movements (Pandiyan et al., 2020) and partially overlapping receptive fields (Kim et al., 2022). Along with stochastic rhodopsin choices (Field et al., 2010) (cf. Fig. 5**B**, inset), microstructural and synaptic variations (Yu et al., 2023), these characteristics should create a stochastically heterogeneous sampling matrix free of spatiotemporal aliasing (Juusola et al., 2017; Kemppainen et al., 2022; Song et al., 2012; Song et al., 2021). By enhancing sampling speed and phasic integration of changing information through heterogeneous channels, ultrafast morphodynamics reduces ambiguity in interpreting sensory stimuli and enhances the brain's "frame-rate" of perception. Such clear evolutionary benefits suggest that analogous morphodynamic processing would also be employed in central circuit processes for thinking and planning actions.

Furthermore, the inherent flexibility of neural morphodynamics using moving sampling units to collect and transmit information should help the brain maintain its functionality even when damaged, thus contributing to its resilience and recovery mechanisms. By using oscillating movements to enhance transmission and parallel information channels streaming overlapping content (Wardill et al., 2012), critical phasic information could potentially bypass or reroute around partially damaged neural tissue. This morphodynamic adaptability equips the

brain to offset disturbances and continue information processing. As a result, brain morphodynamics ensures accurate sensory representation and bolsters neural communication's robustness amidst challenges or impairments.

3.4. Efficiency of encoding space in time

Neural morphodynamics boosts the efficiency to encode space in time (Juusola et al., 2017; Kemppainen et al., 2022), allowing smaller mobile sense organs – like compact compound eyes with fewer ommatidia – to achieve the spatial resolution equivalent to larger stationary sense organs (cf. Fig. 5**C and 6C**). The resulting ultrafast phasic sampling and transmission expedite sensory processing, while the reduced signal travel distance promotes faster perception, more efficient locomotion and decreases energy consumption. Therefore, we can postulate that between two brains of identical size, if one incorporates ultrafast morphodynamics across its neural networks while the other does not, the brain using morphodynamics has a higher information processing capacity. Its faster and more efficient information processing should enhance cognitive abilities and decision-making capabilities. In this light, for evolution to select neural morphodynamics as a pathway for optimising the brains would be a no-brainer.

3.5. Expanding dimensionality in encoding space for cognitive proficiency

But how do insects, with their tiny brains usually containing fewer than a million neurons, often short adult lifespans – with some living just days or weeks – develop sophisticated cognitive abilities? How might neural morphodynamics contribute to balancing genetic predispositions and environmental influences to optimise the use of their tiny brains? The world's object feature space (input space) is vastly larger than the number of neurons (output space) in the insect brain. Therefore, to efficiently map inputs to outputs, their brain circuits must perform space-saving and cost-efficient encoding, where single neurons contribute to multiple network functions (Niven and Chittka, 2010). In other words, the circuits must map object information into combinatorial and distributed feature representations to expand the encoding space. Doing this quickly by phasic (morphodynamic, and thus hyperacute) neural responses expands the networks' dimensionality in encoding space beyond any static system of equal size.

Using this framework, we can consider, for example, that the form/function relationships of the insect central complex (Pfeiffer and Homberg, 2014) (involved in navigation) and mushroom body (Li et al., 2020) (involved in visual learning) circuits are physical manifestations of the algorithms they execute. Genetic information may establish the circuits' x- and y-coordinates within the visual space, while the object's binocular timing differences provide its z-coordinate (depth) and size, reflected as a neural activity pattern on these circuits. As the object moves, this activity pattern moves phasically in sync with the object, assisted by morphodynamics to maintain high spatiotemporal sampling resolution while ensuring the representations remain associable and generalisable. The circuits map the object feature space so that similar objects generate similar activity patterns, while different objects generate distinct patterns – comparable to Kohonen's self-organising neural projections (Kohonen, 2006) and the perceptual colour map in the macaque visual area V4 (Li et al., 2014). The central complex circuits map object position and orientation ("Where"), while the mushroom body circuits map independent chromatic components and context ("What"). Although the varying roles of central brain circuits in navigation and learning are being progressively mapped and modelled (Cope et al., 2017; Dan et al., 2024; Goulard et al., 2021; Green et al., 2017; Heinze and Homberg, 2009; Heinze, 2021; Honkanen et al., 2023; Hulse et al., 2021; Kim et al., 2017; Kim et al., 2019; Lu et al., 2022; Lyu et al., 2022; Mussells Pires et al., 2024; Okray et al., 2023; Pisokas et al., 2020; Scheffer et al., 2020; Seelig and Jayaraman, 2013; Seelig and Jayaraman, 2015), the synchronous encoding patterns and morphodynamic activity across the circuits have not been extensively studied.

Genetic information plays a crucial role in constructing the brain's representation of the world during development and maturation, enabling impressive goal-oriented innate behaviours. Neurophysiological studies have even identified an insect's body coordinates relative to environmental patterns within the seemingly disorganised "neural spaghetti" of optic glomeruli (Wu et al., 2016) However, adult insect brains, such as those of bees, retain plasticity and the capacity for complex learning, even allowing for the transfer of cultural information (see examples in **Text** Box 3). These cognitive feats cannot be adequately explained by conventional input–output models of neural information processing or by neurons' static structure/function relationships. Instead, they demand new holistic paradigms to uncover the underlying code and processes.

Supporting this need for new paradigms, studies in *Drosophila* have shown that the same neural circuits can serve multiple functions depending on the activity state. These circuits efficiently represent the world, plan future actions, and guide behaviours (Chiappe, 2023; Fujiwara et al., 2017; Fujiwara et al., 2022; Tang and Juusola, 2010) by balancing bottom-up sensory inputs and top-down stored executive information to drive behaviour. In other words, *Drosophila* may simultaneously process interacting thoughts and perceptions as phasic morphodynamic activity in the same sparse-distributed memory (Kanerva, 1990) networks. Consequently, it is conceivable that we may soon discover that insect brain networks capable of recognising objects also participate in planning and even dreaming, similar to the bidirectional information flow observed in the human visual cortex (Naselaris et al., 2009; Nishimoto et al., 2011; Willmore et al., 2010).

Moreover, harnessing and fine-tuning genetic information could enable neural morphodynamics efficiently capture sensory input and utilise predetermined retinotopic or body-centric feature maps. This process may facilitate perception and support the emergence of sophisticated insect behaviours, such as learning to differentiate objects using hyperacute stereovision (Kemppainen et al., 2022). We propose that the interplay of morphodynamic, electrical, and chemical processes within neurons 'animates' the brain's representation of the world (**Text** box 3). This dynamic structure/function interaction could generate thoughts and perceptions that continuously shape and transform neural landscapes, enabling impressive cognitive abilities and efficient environmental learning.

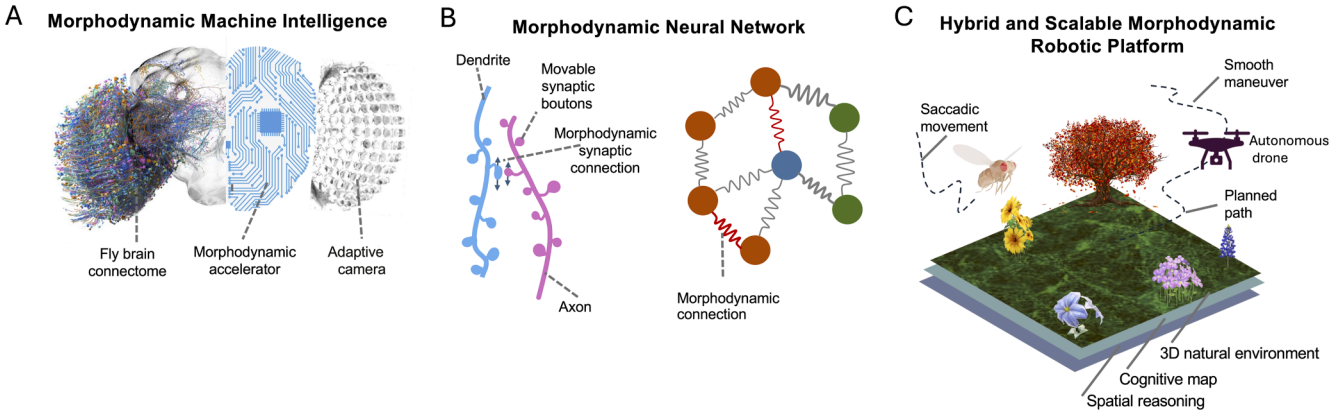
4. Future avenues of research

4.1. Investigating the integration of ultrafast morphodynamics changes

One area of interest is understanding how the brain and behaviour can effectively synchronise with rapid morphodynamic changes, such as adaptive quantal sample rate modifications within the sensory receptor matrix and synaptic information transfer. A fundamental question pertains to how neural morphodynamics enhances the efficiency and speed of synaptic signal transmission. Is there a morphodynamic adaptation of synaptic vesicle sizes and quantities (Juusola et al., 1995) that maximises information transfer? It is plausible that synaptic vesicle sizes and numbers adapt morphodynamically to ensure efficient information transfer, potentially using a running memory of the previous activity to optimise how transmitter molecule quantities scale in response to environmental information changes (cf. Fig. 7**A-B**). This adaptive process might involve rapid exo- or endocytosis-linked movements of transmitter-receptor complexes. Furthermore, it is worthwhile to explore how brain morphodynamics adaptively regulates the synaptic cleft and optimises the proximity of neurotransmitter receptors to optimise signal transmission.

Box 4

Transforming AI with Morphodynamic Principles: Next-Gen Autonomy and Vision. The concept of morphodynamic information processing in the brain has significant implications for developing bio-inspired machine intelligence, vision engines, and neuromorphic accelerators, particularly in autonomous systems. Currently, AI and autonomous vehicles rely heavily on static sensor arrays, networks, and mostly pre-programmed algorithms to interpret the environment and make driving decisions. By emulating the brain's ability to adapt its structure and function to varying stimuli dynamically, engineers can design AI systems that are more responsive and efficient (de Croon et al., 2022; Webb, 2020). For instance, morphodynamic neural computation can greatly enhance sensory and decision-making systems in autonomous vehicles. By integrating morphodynamic principles, these vehicles could develop more adaptive and resilient perception capabilities, allowing them to better detect and respond to sudden changes in their surroundings, such as unexpected pedestrians or obstacles. They could dynamically adjust their information processing to prioritise the most critical inputs, thereby improving the robustness and versatility of autonomous machines in complex, unpredictable environments.



(**A**) Morphodynamic principles, particularly those that mimic biological photoreceptors, have the potential to revolutionise machine vision systems. By incorporating adaptive, rapid, and active sampling strategies observed in nature (Fenk et al., 2022; Geurten et al., 2014; Juusola et al., 2017; Kemppainen et al., 2022; Kemppainen et al., 2022; Land, 2009; van Hateren and Schilstra, 1999); morphodynamic-driven digital cameras could achieve unprecedented levels of spatial and temporal resolution while maintaining low computational power and requiring fewer light sensors (Medathati et al., 2016; Serres and Viollet, 2018; Song et al., 2013). Combining these principles with multiscale active sampling from eye, head, and body movements would enable machines to perceive and interpret their surroundings with greater efficiency and coherence, even under highly variable lighting and environmental conditions (Land, 2009; MaBouDi et al., 2021; MaBouDi et al., 2023). For example, a morphodynamic-inspired vision system could adjust its sensitivity and focus in real time, similar to how biological visual systems adapt to different lighting conditions and movement speeds. This capability would be particularly valuable in autonomous vehicles, drones, and robots, where quick and precise environmental interpretation is crucial for safe and effective operation.

(**B**) Morphodynamic neural computation also offers a novel approach to developing neuromorphic models by introducing dynamic elements into what has traditionally been a largely static framework. In conventional neuromorphic models, neural connections – particularly synaptic connections – are often assumed to be fixed or to change slowly over time based on pre-defined learning rules (Schuman et al., 2022). However, this static assumption limits the models' ability to fully capture the rapid and adaptive nature of biological neural networks. By incorporating the concept of synaptic connection movements – where synapses can shift, adapt, or reconfigure quickly in response to stimuli – morphodynamic neural computation adds a complementary layer of information processing (Wang et al., 2024). These fast, dynamic adjustments allow the neural network to actively modify its structure in real-time, enhancing its ability to process complex and variable sensory inputs. This additional layer of morphodynamic processing enables the network to encode and transmit information not only through the strength of synaptic connections but also through their morphodynamic rearrangement (**B**, right). This dynamic behaviour mirrors biological processes, where synaptic plasticity and structural changes contribute to learning and memory. In neuromorphic models, these morphodynamic elements can lead to improved performance in tasks requiring rapid adaptation, such as real-time decision-making and pattern recognition in unpredictable environments. By incorporating these principles, neuromorphic systems can become more flexible and responsive, offering a richer and more nuanced approach to artificial neural computation.

(**C**) Furthermore, integrating fast adaptation, efficient processing, and predictive coding mechanisms observed in neural morphodynamics into AI and robotics could significantly enhance the development of anticipatory and context-aware systems (Millidge et al., 2022; Rao, 2024). By leveraging dynamic synchronisation and phasic information sampling, these bio-inspired AI models would not merely respond to stimuli but also anticipate future states, facilitating proactive decision-making and more seamless interactions with their environment. For instance, the predictive coding aspects of morphodynamic computation could enable autonomous vehicles to foresee rapid environmental changes and accurately predict the movements of other vehicles and pedestrians, resulting in smoother navigation and enhanced safety – an improvement over current AI models that typically rely on static processing frameworks and struggle with real-time adaptation and prediction. Similarly, in robotics, morphodynamic neural computation could revolutionise motor control and sensory integration (Pfeifer et al., 2007; Rao, 2024). By emulating the brain's ability to synchronise and adjust neural responses to varying stimuli, robots could achieve more fluid and natural movements. For example, a drone equipped with morphodynamic-inspired control systems could dynamically modulate its grip strength and precision in response to the texture, shape, and spatial relationship of objects, similar to how humans instinctively adjust their motor output based on sensory feedback (Greenwald, 1970). Furthermore, incorporating predictive coding mechanisms would enable such robots to anticipate the outcomes of their actions, promoting more coordinated and efficient interactions within three-dimensional environments and enhancing navigational capabilities.

4.2. Genetically enhancing signalling performance and speed

Another avenue of research involves investigating the possibility of genetically enhancing signalling performance and speed to control behaviours. This exploration can delve into how genetic modifications may improve the efficiency and speed of signal processing in the brain. By manipulating genes to change neurons' physical properties, such as increasing the number of photoreceptor phototransduction units or neurotransmitter-receptor complexes or accelerating their biochemical reactions, it may be possible to enhance the performance and speed of signalling (Juusola and Hardie, 2001; Song and Juusola, 2014), ultimately influencing behavioural responses. By further investigating these aspects of brain morphodynamics, we can gain deeper insights into the mechanisms underlying efficient information processing, synaptic signal transfer, and behavioural control.

For example, CRISPR-Cas9 gene-editing, by adding, removing, or altering specific genes associated with molecular motors or mechanoreceptive ion channels within neurons, provides means to elucidate these genes' functions and their roles in neural morphodynamics.

4.3. Neural activity synchronisation and perception enhancement

It is crucial to understand how neural morphodynamics synchronises brain activity within specific networks in a goal-directed manner and to comprehend the effects of changes in brain morphodynamics during maturation and learning on brain function and behaviour. Modern machine learning techniques now enable us to establish and quantify the contribution of brain morphodynamics to learning-induced structural and functional changes, and behaviour.

For instance, we can employ a deep learning approach to study how *Drosophila*'s compound eyes use photoreceptor movements to attain hyperacuity (Razban Haghighi, 2023). Could an artificial neural network (ANN), equipped with precisely positioned and photomechanically moving photoreceptors to process and transmit visual information to a lifelike-wired lamina connectome (cf. Figs. 2 and 4), reproduce the natural response dynamics of real flies, thereby surpassing their optical pixelation limit? By systematically altering sampling dynamics and synaptic connections in an ANN-based compound eye model, it is now possible to test whether the performance falters without the realistic orientation-tuned photoreceptor movements and connectome and the eye loses its hyperacuity.

Neural morphodynamics mechanisms can enhance perception by implementing biomechanical feedback signals to photoreceptors via feedback synapses (Zheng et al., 2006) to improve object detection against backgrounds. An object's movement makes detecting it from the background easier (Kapustjansky et al., 2010). When interested in a particular object in a specific position, could the brain send attentive (Tang and Juusola, 2010; van Swinderen, 2011) feedback signals to a set of photoreceptors, in which receptive fields point at that position, to make them contract electromechanically, causing the object to 'jump'? This approach would enhance the object boundaries from its background (Chittka and Spaethe, 2007). Such biomechanical feedback would be the most efficient way to self-generate pop-up attention at the level of the sampling matrix.

5. Conclusion and future outlook

Theory of neural morphodynamics offers a new perspective on brain function and behaviour, providing a unified framework that shifts from *reductionism* to *holistic constructionism*. It utilises observed neural signals – both micro- and macroscopic – as information carriers (de Polavieja et al., 2005; Juusola and de Polavieja, 2003; Juusola et al., 2007; Juusola et al., 2017; Kemppainen et al., 2022) rather than their assumed abstractions. This approach links neural structures to functions in space–time across multiple scales for a deeper understanding of the brain. By addressing the key questions and conducting further research, we can explore the applications of ultrafast morphodynamics for neurotechnologies (see **Text** Box 4). These applications may enhance perception, improve artificial systems, and lead to the development of biomimetic devices and robots capable of sophisticated sensory processing and decision-making.

CRediT authorship contribution statement

Mikko Juusola: Writing – review & editing, Writing – original draft, Visualization, Funding acquisition, Conceptualization. **Jouni Takalo:** Writing – review & editing. **Joni Kemppainen:** Writing – review & editing, Visualization. **Keivan Razban Haghighi:** Writing – review & editing. **Ben Scales:** Writing – review & editing. **James McManus:** Writing – review & editing. **Alice Bridges:** Writing – review & editing, Visualization. **HaDi MaBouDi:** Writing – review & editing, Visualization. **Lars Chittka:** Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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