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Forum

Bees, blindsight, and consciousness

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Blindsight patients lack conscious visual perception yet perform visual tasks effectively, suggesting many animals may similarly rely on non-conscious vision. Here, we discuss how to investigate visual consciousness in miniature brains, using bees as a case study. This new endeavor can reveal the minimal neural requirements for visual awareness.

Visual consciousness and its paradoxes

One of the most intriguing aspects of consciousness is our visual experience. We perceive detailed visual scenes populated by objects with defined spatial relationships, integrating properties such as color, shape, and motion into a unified percept. However, this subjective image is far from a veridical representation of the external world. Much of our conscious perception is 'made up' by the brain, influenced by attention, and susceptible to illusions. We might assume that adaptive behaviors, like obstacle avoidance, detection of rewards and threats, and recognition of conspecifics, would be impossible without conscious visual experience. However, several visual functions can occur without conscious awareness [1]. This paradox prompts the inquiry into the minimal neural architectures required to sustain **visual consciousness** (see Glossary).

Among invertebrates, bees provide a revealing case. Despite their miniature brains, bees perform complex visual and cognitive tasks previously considered exclusive to vertebrate species, including abstract learning and cross-modal generalization. These capacities and a well-mapped neuronal organization offer a valuable opportunity to explore how visual awareness might emerge from compact nervous systems [2].

We outline behavioral paradigms that dissociate conscious from non-conscious visual processing in human and non-human primates. We propose possible ways to adapt these paradigms for bees. Finally, we summarize comparative neuroanatomy and computational evidence to derive testable predictions about the minimal neural principles for conscious vision across species.

Insights from blindsight

Distinguishing between sophisticated non-conscious processing and genuine visual awareness remains challenging. To this end, the neuropsychological condition of 'blindsight' provides an experimental window into residual visual processing without awareness [3]. Patients and non-human primates with damage to the primary (striate) visual cortex (V1) experience clinical blindness in the corresponding visual field, yet preserve a range of residual visuomotor abilities. When instructed to 'guess', blindsight subjects can localize stimuli, discriminate motion and wavelength, and avoid obstacles, demonstrating that a broad spectrum of visual behaviors can occur outside conscious awareness [3]. This raises the possibility that non-conscious mechanisms, akin to those supporting blindsight, might mediate adaptive visual behaviors in other species, including animals with compact nervous systems and image-forming eyes.

Glossary

Cross-modal binding: a cognitive process by which sensory information from different modalities, such as visual and tactile stimuli, is combined into coherent percepts.

Opt-out task: a behavioral paradigm in which subjects can decline a perceptual decision when uncertain or unaware of the stimulus. Typically applied to non-human primates and rodents, this method assesses confidence and subjective certainty, as subjects opt out more frequently when stimuli are ambiguous or near the perceptual threshold.

Perceptual rivalry: a phenomenon in which perception alternates between competing interpretations of ambiguous or conflicting visual stimuli, reflecting shifts in neural representations and conscious experience. For example, if one eye is presented with a face and the other with a house, the subject sees alternations of either image at a time.

Post-decision wagering: a behavioral measure of perceptual awareness and confidence in a decision, in which subjects place bets on the accuracy of their judgments after making a decision. The wager amount reflects implicit confidence, with higher wagers indicating greater certainty. This approach links betting behavior to awareness of decision quality.

Second-order commentaries: behavioral measures where subjects non-verbally comment on their perceptual experience. For example, monkeys with V1 damage can localize stimuli in their affected field and yet categorize them as 'not seen' or equivalent to blank trials.

Visual consciousness: the subjective experience and explicit access to visual information, including its qualitative aspects. It is a form of primary or perceptual consciousness, distinct from higher-order self-awareness and from general states such as wakefulness or sleep.

However, non-conscious abilities preserved in blindsight tend to lack behavioral flexibility, context-dependent integration, **cross-modal binding**, perceptual constancy, and generalizability across different situations. By contrast, bees excel in many tasks where primates with blindsight and V1-independent vision often fail. They can learn and recall complex visual patterns, group together elements flexibly depending on context, and discriminate stimuli based on abstract relational properties, irrespective of specific physical features [4]. Bees demonstrate cross-modal object recognition, transferring learned information between vision and touch [2]. Thus, while blindsight reveals the limits of visual behavior without awareness, bees demonstrate how small brains can support visual and cognitive capabilities typically considered to depend on conscious processing (Figure 1). These apparent discrepancies

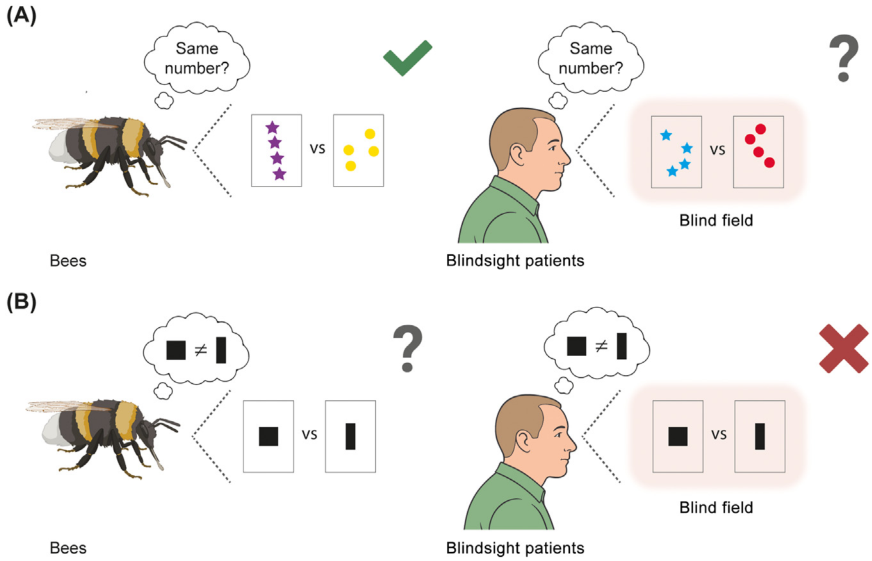

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Figure 1. Behavioral tasks illustrating comparative visual functions in bees and primates. (A) Numerosity invariance: bees can successfully discriminate between groups of items based on numerosity, independent of variations in the arrangement, color, or shape of individual elements, demonstrating flexible abstraction and feature constancy. Equivalent tests have not yet been conducted in human or non-human primates with blindsight, and we predict chance-level performance given limited constancy and integration across multiple items. (B) Efron figures: blindsight patients fail to discriminate Efron shapes, which differ in length-to-width ratio but not in the orientation of component lines. Such a task remains untested in bees, but we predict successful performance owing to their demonstrated capacity for context-dependent visual learning and generalization.

caution against assuming that a miniature nervous system necessarily precludes visual awareness.

Adapting behavioral paradigms to probe visual consciousness in insects

We propose that direct examination of visual consciousness in bees lies within the reach of contemporary neuroethology. Insects are separated from vertebrates by more than 500 million years of evolution. Hence, structural or functional similarities between their visual systems likely reflect convergent evolutionary solutions to shared ecological demands, rather than homology.

Nevertheless, existing paradigms to probe potential dissociations between conscious and non-conscious perception in mammals [5] can be adapted to insects. **Perceptual rivalry** involves alternating perception toward ambiguous or conflicting stimuli, like Necker's cube or the vase-face illusion, or when two images that cannot be fused are simultaneously presented to each eye. Rivalry occurs in flies and is accompanied by alternating activity in visual neuropils that precedes behavioral switches [6]. Likewise, spatial cueing paradigms yield opposite outcomes depending on stimulus awareness. Consciously perceived cues presented at the opposite location of the subsequent target improve performance. By contrast, non-consciously processed cues slow down target detection, demonstrating distinct modes of visual processing dependent on awareness. Similar dissociations occur in humans and primates [7], suggesting that careful behavioral testing could reveal analogous distinctions in insects.

Other confidence-based measures have been successfully applied to primates and rodents. Common to these methods is the request to indicate confidence in judgments, approximating visual awareness by implicitly measuring subjective certainty beyond mere accuracy. In **second-order commentaries** (commentary-key method), monkeys classify visual stimuli presented to blind fields as 'not a light', demonstrating implicit perception without conscious experience [5]. **Opt-out tasks** allow subjects to decline challenging perceptual discriminations when uncertain about their choice [8]. In **post-decision wagering**, animals can be trained in tasks where they place bets – larger or smaller amounts – on the accuracy of their perceptual judgments, directly linking wager magnitude to their implicit evaluation of decision quality. These paradigms can be adapted for free-flying bees by associating confidence with differential reward choices. Demonstrating a dissociation between accuracy and confidence would provide a comparative signature of conscious access to visual content.

Neural substrates and comparative anatomy

At the neural level, the idea that insect brains might generate visual consciousness appears counterintuitive, particularly as primates lose visual awareness following lesions restricted to V1, a region comprising only a small fraction of the cortical surface (approximately 3% in humans and up to 15% in macaques). Bees have miniature brains containing about one million neurons within just 1 mm^3 [2] (Figure 2). For comparison, the human brain comprises about 86 billion neurons with a volume of approximately 1300 cm^3. Bee neurons are densely packed into discrete neuropils structured in clusters (ganglia), lacking the laminated cerebral cortex characteristic of mammals. Evolutionary divergence is evident even within mammals, as V1 lesions severely disrupt vision in primates. This likely reflects 'encephalization of function', whereby visual capabilities migrated from ancestral subcortical structures to more recently developed cortical regions.

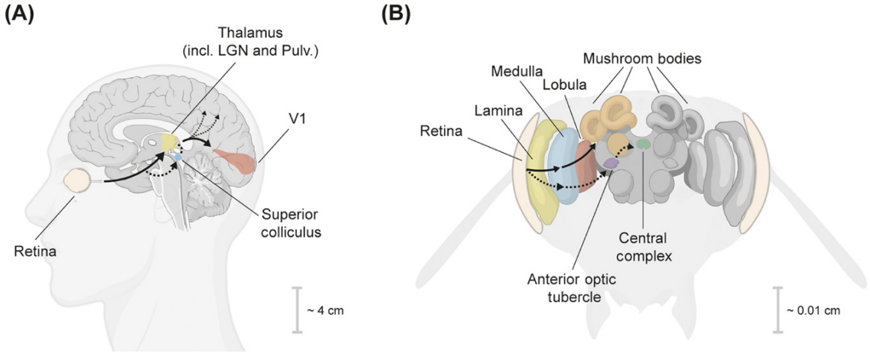

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Figure 2. Comparative visual pathways in the human and bee brains. (A) Human brain (sagittal view). In primates, the primary visual pathway necessary for conscious vision originates from the retina and projects to V1 via the lateral geniculate nucleus (LGN) of the thalamus (unbroken arrows). V1-independent routes include direct projections from the retina to the superior colliculus in the midbrain and to the pulvinar in the posterior thalamus, which in turn relay signals to multiple extrastriate visual areas (broken arrows). The superior colliculus also projects to the koniocellular layers of the LGN that transmit information to the middle temporal complex, supporting additional V1-independent processing. (B) Bee brain (frontal view): in bees, visual information flows from the retina through a series of optic neuropils (unbroken arrows) – the lamina, medulla, and lobula – that are retinotopically organized and partly laminated. The medulla integrates local visual features such as motion, contrast, and color, while the lobula performs higher-order computations related to object recognition and visuomotor transformations critical for approach and avoidance behaviors. From the lobula, processed signals reach the mushroom bodies – expanded associative centers for multisensory integration, learning, and memory. Additional visual pathways project to the central complex – a midline hub connecting sensory and motor systems – via the anterior optic tubercle, supporting further spatial orientation, attentional selection, and multimodal integration (broken arrows).

At the macro-architectural level, the behavioral complexity observed in bees likely results from extensive convergence and integration of parallel computations within central neuropils, notably the mushroom bodies, rather than from independent and domain-specific modules [4]. This configuration is consistent with cognitive theories proposing that consciousness emerges when the output of first-order representations becomes widely accessible to higher-order processing systems [1]. At the cellular level, studies in mammals highlight that pyramidal neurons support the sustained dynamics critical for conscious processing, such as separating forward from backward information flow [9]. Though bees lack pyramidal cells, their Kenyon cells in the mushroom bodies fulfill analogous integrative cognitive functions. Thus, rather than anatomical homologies, functional analogies suggest that recurrent and integrative architectures can sustain comparable visual cognition across species.

Convergent solutions for visual processing

Despite differences in scale and divergent anatomy, insect and vertebrate visual systems share computational principles and exhibit modular architectures organized around hierarchical feature extraction and recurrent integration [10]. Insect neuropils, such as the lobula, and vertebrate midbrain structures, like the tectum (the superior colliculus of mammals), both operate as third-order visual structures, encoding motion, looming, and spatial localization, essential for visuomotor control [11].

Accordingly, blindsight can persist even when the entire cortical mantle in one hemisphere is removed, with the superior colliculus as the only remaining target of retinal projections [3]. However, V1 lesions disrupt the recurrent broadcasting required for conscious access, confining subcortical processing to non-conscious behavior. In insects, dense feedback loops between visual and central brain neuropils might permit the global availability of visual representations, possibly achieving functional parallels to cortical broadcasting with far fewer neurons to sustain a proto-form of visual awareness [12].

Computational insights from neural networks

Computational neuroscience models, inspired by structural and functional principles of the primate and insect visual systems, offer opportunities to test how visual functions and neural representations can arise from a limited set of computational principles. For example, a computational model of the superior colliculus spontaneously replicates blindsight-like properties, exhibiting tuning to low spatial frequencies and selective biases characteristic of non-conscious visual processing [13]. Similarly, bio-inspired models of insect vision demonstrate that minimalistic neural architectures can achieve sophisticated tasks like visual generalization and stimulus location invariance [2]. These findings converge on a principle of computational parsimony and suggest fundamental principles in processing efficiency in how natural brains encode visual features; namely, deriving higher-order visual representations from remarkably simple, recurrent computational mechanisms.

Concluding remarks

Bees offer a unique opportunity to define the minimal neural requirements for visual awareness in compact brains with limited neuronal resources. An integrative framework combining behavioral assays, neural imaging techniques, and computational modeling promises to advance our understanding of fundamental principles underlying consciousness, illustrating commonalities and divergences across species and evolutionary trajectories.

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Declaration of interests

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