Title

Insect lifestyle and evolution of brain morphology

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Highlights

Insect lifestyles often correlate with variations in different regions of their brain

Co-option and subtle tuning of brain structures might mask neural adaptations

Current methodological advances will reveal subtle brain adaptations to lifestyle

Stronger evidence will come from comparative works informed by lifestyle features

Abstract

Insect lifestyles are extremely diversified and have important consequences for brain function. Lifestyle determines the resources and information that brains have access to, but also those that are required, to produce adaptive behaviors. Most of the observed adaptations of brain morphology to lifestyle are related to the first stages of sensory information processing (e.g. adaptations to diel habits). However, morphological signatures of lifestyles related to higher order processing of information are more difficult to demonstrate. Co-option of existing neural structures for new behaviors might hinder the detection of morphological changes at a large scale. Current methodological advances will make it possible to investigate finer structural changes and might shed light on whether or not some lifestyles (e.g. eusociality) require morphological adaptations.

Introduction

Insects offer an extraordinary opportunity to study brain evolution: they are extremely abundant and diversified, and possess miniaturized brains that can teach us about the essential structures that process information and coordinate behavior [1]. Lifestyles categories (diurnal/nocturnal, solitary/social, etc.) are organized around common ecological factors and behavioral strategies, and have an important effect on brain function: they determine the resources and information that brains need and have access to in order to produce adaptive behaviors (Fig 1A). Within the limits imposed by each species' phylogenetic history, physiological (e.g. neuromodulation) and morphological (e.g. circuit remodeling) adaptations may show common trends in animals sharing a given lifestyle. This review will focus on the second, which are typically easier to compare across species. We will discuss the evidence found for some lifestyles and suggest possible approaches for tackling lifestyles without clear links to brain morphology. In vertebrates, some neuroanatomical changes do correlate with different lifestyles related to diet, sociality or habitat [2–5]. The great diversity of insects poses a considerable challenge to find common trends, but also opens a unique opportunity to uncover general features governing brain morphology.

The insect brain is a mosaic of sub-regions involved in different functions, from sensory and higher-order information processing to coordination of behavior [1] (Fig 1B). Despite a considerable morphological variability in size, shape and organization, a common plan in the insect brain allows us to identify comparable sub-regions across taxa [6–9]. After controlling for the phylogenetic history, variations in relative investment in different subregions [8,10–12], internal organization [13–17], connectivity between regions [18] and neural circuits [19] might reflect neural adaptations to the species' lifestyle.

To elucidate which (if any) morphological traits vary as an adaptation to insect lifestyle, intra-specific approaches take advantage of lifestyle changes over the course of an individual's life, across specialized morphs in polymorphic species, or through experimental manipulations. Other approaches are based on comparative analysis of species with different lifestyles. Intra-specific studies might give valuable insight about the flexibility of brain traits, but inter-specific ones, carefully performed in a variety of taxa, will eventually identify morphological variations selected through evolution. For a more successful outcome, both approaches need to complement each other and build on the current knowledge of the insect brain function at physiological and morphological levels, especially in model insects, where more tools are available [7,20–23].

Successful studies require a clear link between a lifestyle and a particular area or circuit of the brain. Given our limited understanding of brain function, this link is easier to establish for brain regions and functions in the first stages of sensory processing (Fig. 1A). The clearest trends have been found in these regions, but thanks to the current technical advances (in imaging, transcriptomics, connectomics, etc.) more challenging links between lifestyle and morphological and molecular features of the brain are starting to be disentangled.

Primary sensory processing as a strong predictive factor

The relationship between visual information and neuroanatomical adaptations provides a good example of clear co-evolution of lifestyles and brain morphology. Light availability strongly affects investment in visual processing structures in two main ways. First, overall investment in visual neuropils is higher when there is more light, a trend linked to lifestyles both through habitat and diel habits. We find, for example, that above-ground army ant species (whose visual system is poorly developed) have larger optic lobes (primary visual processing neuropils; OL) and mushroom bodies (high order, often multisensory, processing neuropils; MB) relative to overall brain size than the subterranean ones [24]. Some subterranean ants and cave beetles even completely lack eyes and visual neuropils [25,26]. Regarding light availability above ground, many species adapted to low light conditions (nocturnal and crepuscular vs diurnal) invest less in visual neuropils and more in olfactory ones [10,8,11,12]. This stronger investment in other senses, such as olfaction, may be a way to compensate the lack of light with other sources of information and/or a consequence of trade-offs within parts of the nervous system. Such trade-offs might be suggested by a comparative study in crepuscular *Drosophila* species that shows a negative correlation between the sizes of the OL and the antennal lobe (primary olfactory processing neuropil, AL) [27]. However, there is not enough ecological and behavioral information about these species (such as diel habits or sensory modalities involved in host plant detection) to rule out a compensatory role.

A second general trend is that animals exposed to low light levels develop enhanced sensitivity [28], which leads to a higher relative investment in the first visual stages. The lamina is the first OL neuropil, and it is important for contrast and motion detection. While the relative size of the rest of the OL is smaller in nocturnal/crepuscular than in diurnal species, the lamina's relative size is not reduced and sometimes is even larger [10,29]. This different investment in the first and subsequent visual processing stages might be facilitated by a peculiarity of the synaptic organization in the lamina of some nocturnal and crepuscular species, whose lamina monopolar cells connect more cartridges than in diurnal ones [30,31], supporting a neural summation of the light signal and enhancing sensitivity [32]. This neural summation might reduce the lamina's output to the downstream regions and therefore their size, explaining why some insects with large eyes and large lamina have smaller than expected medulla and lobula [8,29]. A comparative study in dung beetles combined anatomy with behavioral manipulations showed more adaptations of the lamina to nocturnal lifestyle. By forcing them to navigate in the non-preferred activity period, the study revealed that the diurnal species use celestial bodies at day and night (the sun and the moon) and nocturnal species preferentially use polarized light at night and the sun at day [33]. Interestingly, only the nocturnal species seem to present a particular lamina region, the lamina dorsal rim area, related to polarization vision in other insects [8].

Besides inter-species comparative studies, analyses of individuals of the same species show similar trends. In social insects, individuals specialized in tasks inside the nest have smaller OL than those that also labor outside [34–37]. In species where there is a maturity transition of individuals between under- and above-ground activities, brain volumetric and synaptic modifications in primary and/or high order visual processing brain regions also take place [38–40]. Even experimental manipulations might produce the same effect: Light deprivation during adult maturation leads to reduced OL volumes in *Drosophila melanogaste*r [41].

Besides light levels, other features of an insect's visual landscape can be traced to morphological adaptations. One of these features (which probably interacts with the complexity of the environment) seems to be the speed at which interesting stimuli move. Many insects that need fast and accurate reactions seem to invest more heavily in vision, which relays near-instantaneous and precise information about the environment, and has fewer constraints than other fast senses such as mechanosensation, which requires physical connection. Vision is therefore very relevant for many predatory insects, and their visual neuropils often present modifications adapted to their behavioral strategies. Mantises, capable of stereopsis (3D vision), have large eyes and large OL with highly differentiated medulla and lobula complex [17]. These neuropils host neurons sensitive to binocular disparity and their connections to the central brain and the contralateral lobula complex constitute a neuronal support for stereopsis [42]. Dragonflies and damselflies also have very large eyes and OL. Their eye morphology and hunting strategies are very different, but the anatomy of their target-selective descending neurons is very similar, suggesting a robust adaptation to predation of this conserved visual circuit [43]. Even in ants, which rely mainly on olfaction, predatory species are highly visual [26,44], with their medulla showing a columnar structure observed in other visual insects but not common in other ants [45]. Some beetle larvae are ferocious predators presenting specialized visual systems and hunting strategies. Larvae ambushing their prey present a lobula plate equipped with motion sensitive neurons, which is absent in species with other strategies [46]. Additionally, flying insects seem to highly rely on vision: In ants, winged individuals (reproductive males and females) have bigger optic lobes than wingless walking workers [47,48]. While compelling, this evidence about the influence of predatory and flying lifestyles on vision are largely based on single-species observations, and we still lack comparative studies with carefully controlled phylogeny that would confirm the link.

All these studies have in common a clear understanding of how a lifestyle influences information availability and needs, and a clear link with first-order sensory processing brain regions. We will next discuss the challenges involved when dealing with more complex relations between lifestyles and brain morphology.

Beyond primary sensory processing

Sometimes it is difficult to identify the brain structural changes that might accompany some lifestyles. There are two main challenges: 1) some lifestyles cannot be easily dissected in simple quantifiable components, and 2) the neural substrate changes for a given behavior/lifestyle may be very subtle.

The first challenge is the difficulty of dissecting complex lifestyles in components that can be traced to particular hypotheses. This is the case, for example, of the application of the social brain hypothesis in insects. This hypothesis states that the additional sources of information related to sociality might increase the cognitive load on the individuals, and therefore, the investment in brain regions to process them. In vertebrates, group size and pair bonding was associated with larger brains [2]—although this hypothesis is contested in primates: other factors, such as diet, are better predictors of brain volume than social variables [4]. In insects, some evidence supports the idea that social species process more information; for example, solitary bees invest less in antennal sensilla than social species [49]. However, individuals in a group can specialize in different tasks or use simple collective strategies, so at high levels of sociality we might encounter the opposite trend, with reduced brain structures [50]. This is consistent with findings in monomorphic (similar size and morph for all the individuals of the worker caste) Dolichoderinae ant species, in which workers from smaller colonies invest more in the AL than those from larger colonies [51]. Most research on this topic has focused on the MB, which was suspected to reflect social complexity due to its great development in social Hymenoptera and Dictyoptera. However, some solitary species also possess elaborated MB [52] and comparative studies indicate that there is no clear correlation between MB size and social complexity [50,53].

Social complexity has many different features, and many have suggested that comparative approaches must focus on single components (parental care, reproductive division of labor, polymorphism, etc.) and on functional neuronal traits (circuits, cells and synapses instead of only relative neuropil volumes), without forgetting alternative or complementary hypotheses (such diet shifts or foraging behavior) [54,55]. Successful results have been obtained by, for example, focusing on individual specialization through division of labor. In bees, brain differences between males and females are less prominent in solitary species than in eusocial ones [56,57]. In primitively eusocial bees and wasps, where reproductive division of labor is achieved by dominance, queens have bigger MB than workers [58,59], but there is an opposite tendency in more advanced eusocial species [48]. In monomorphic acacia ants, defensive workers show reduced MB in comparison with leaf collectors [60]. Ant polymorphic species provide even more examples of brain specialization [36,48,61,62].

The second challenge consists of dealing with radical behavioral changes with little morphological signature. Some of these cases result from the co-option of sensory structures and neural circuits that were already present for related behaviors and could be adapted with minimal tuning.

Some possible co-options or circuit tunings might have happened for the adaptation to social lifestyles. The expansion of the MB seems to precede the apparition of sociality [52], but it might have been instrumental for it. For example, central place foraging requires a strong capacity for spatial learning, which is supported by the MB processing. The AL might be another good example: they are present in most insects, but they play a fundamental role for the recognition among colony members (through detection of cuticular hydrocarbons). Ants and hornets, from lineages where eusociality evolved independently, seem to share the same olfactory subsystem detecting long-chain hydrocarbons, suggesting a possible common origin of this system in the solitary ancestor [63].

Another example can be found in lifestyles requiring long distance migratory behavior, which likely requires adjusted sensory and motor control systems allowing a sustained and oriented navigation. The central complex (CX), anterior optic tubercles (AOTU) and lateral complex (LX) are involved in navigation and compass orientation. Intraspecific comparisons in locusts and butterflies show that the CX (or the relative investment in some parts of it) is larger in mass migratory than in solitary and in non-migratory individuals [64,65]. At the inter-specific level, a comparative study between migratory and non-migratory moths shows that their CX is very similar, and instead, some differences exist in the AOTU and the LX [66], the input and output relay stations of the CX. These results suggest that, instead of investing more on some structures, migratory insects might have co-opted and/or tuned sensory and motor circuits involved in general navigational abilities, required by all insects.

Conclusions and perspectives

Understanding how brain morphology and lifestyle diversity have co-evolved requires dissecting insect lifestyle in its different requirements for information processing and the analysis of their effects on measurable neural traits. Volumetric analyses have provided substantial advances and insight in this topic. However, general trends among taxa are not always observable with this methodology, either because of phylogenetic constraints or because adaptations might be physiological or take place at other morphological levels (such as the connectivity between structures, neural circuits or even small synapsis remodeling).

This field is currently experiencing the opening of new opportunities thanks to methodological advances in imaging [67,68], connectomics [22,23,69] or transcriptomic [70], which might allow us to detect more subtle changes and common patterns across lifestyles. Additionally, the creation of databases of neuroanatomical atlases of different species (such as www.insectbraindb.org) and the comparative study of insect life histories with phylogenetic approaches constitute the perfect ground to disentangle how brain morphology varies adaptively with insect lifestyle.

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Figure and figure caption

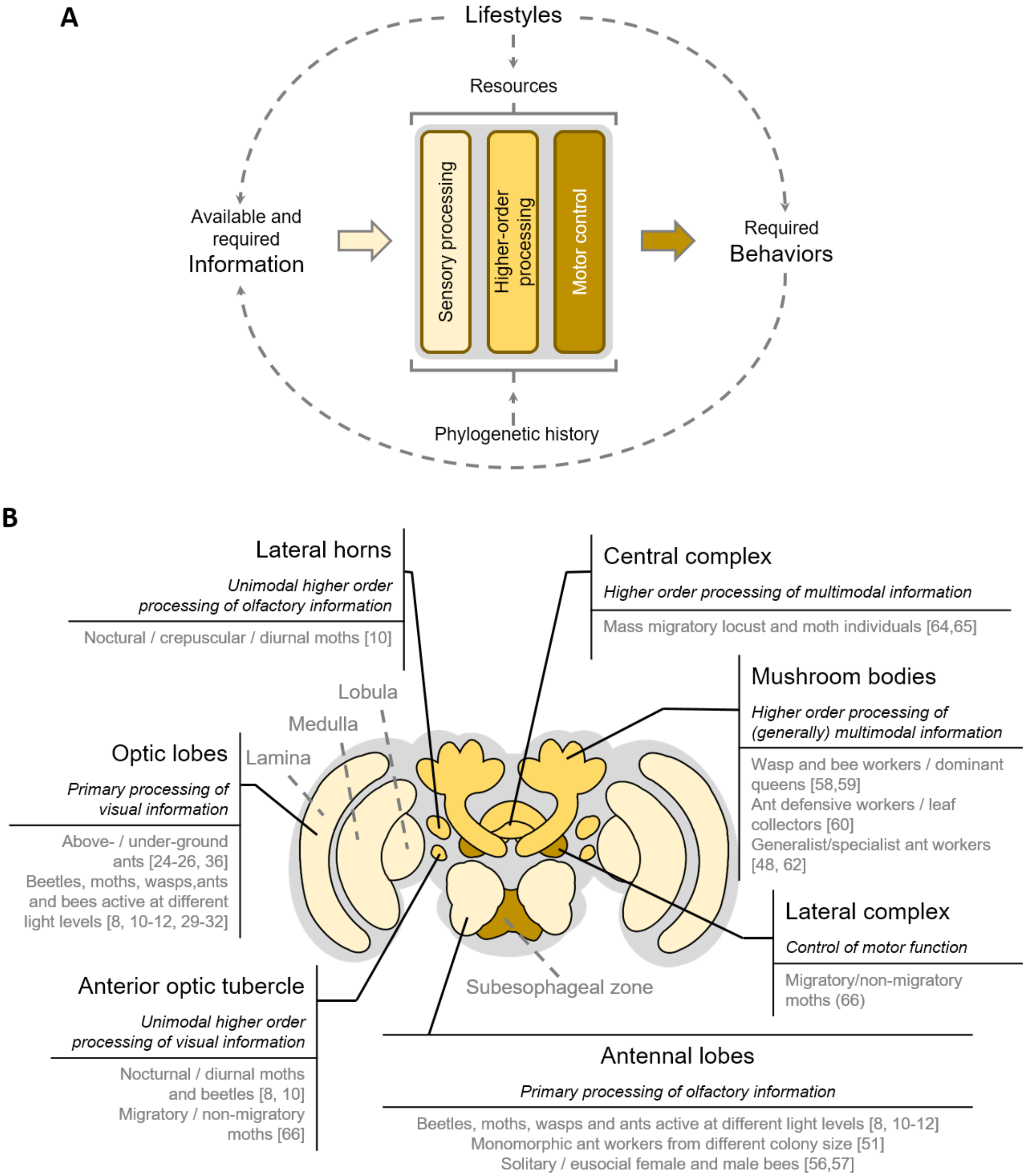

Figure 1. A. Conceptual schematic of relevant elements linking lifestyles with brain morphology

and function. Brains process information through different steps (sensory processing, high-order processing, and motor control) to produce behaviors. Lifestyles affect the information that is available, the behaviors required for survival, and the information needed to produce them. Additionally, lifestyles also limit the resources to which the animal has access and that are needed to sustain the brain. Finally, brain morphology and function is also affected by the constraints imposed by the phylogenetic history of the animal. **B**. Simplified representation of an insect brain morphology and related functions (based on bee brain, but the same structures are present in most insects). The most studied regions are highlighted and linked to a general description of their information processing. In grey, examples of found modifications of brain regions according to lifestyle and their references.