

The social brain of ‘non-eusocial’ insects

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Decisions are seldom entirely devoid of social influence. Even in organisms that have traditionally been considered non-social, the social environment plays an important role in mediating behavior. Here we review the current knowledge regarding the neural basis of social behaviors in non-eusocial insects, with a particular focus on fruit flies, cockroaches and locusts. Each are shown to offer valuable, and complementary, insights into how social behavior is mediated at the neural level. The presented studies demonstrate that social cues, which are integrated in primary sensory areas, exert a considerable influence on behavior. Further studies with these models, and others, will provide important insights into the diversity of social behaviors, and into the way that these are encoded in dedicated brain and neuronal structures.

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Introduction

The interactions between an individual and its environment is intrinsic to the behavior of all living organisms, and crucial for their survival. A special case is that of the interaction between an individual and its social environment. Individuals both influence, and are influenced by, others, and this recursive relationship can result in behavior being increasingly coupled. In the context of the current short review, we examine the interplay between individual behavior and their non-social and social

environment, asking specifically: How are the interactions between the individual and its environment influenced by that individual’s interactions with the social and non-social environment; and how is this reflected in the neuronal substrates of the individual’s behavior.

It is important to note that the term ‘social environment’ is a broad one, and can relate to current or past, long-lasting or transient, social experiences. The social experiences provide both immediate contextual factors and selective pressures on the expression of adaptive behavioral responses [1]. As such, individual behavior can be profoundly shaped by the perceived social environment. However, establishing direct causal relations between the social environment and a modification in neuronal properties or neural circuitry remains a challenging task, as the timescale is often an evolutionary one and thus the interactions cannot be experimentally demonstrated.

The effect of the social environment is most pronounced in animals exhibiting highly coordinated collective behavior [2,3]. Collective behavior is generally referred to as a special type of behavior involving multiple organisms, and which is emergent or self-organized. It is a feature of the collective (the swarm, flock, shoal, etc.) that it is based on local interactions amongst its members. Hence, the above noted intricate three-way interface (individual, non-social and social environment) is instrumental in affecting the behavior of both the individual and the group.

It is not surprising that most research in insects on the interactions between individuals and their social environment has been limited to the eusocial insects, and in particular ants, bees and wasps (see recent reviews [3–5]). However, as will be highlighted here, important insights can be also obtained from a comparative investigation of different taxa (see also [6,7]), and we have therefore chosen to focus here on three of the best-studied non-eusocial insects, fruit flies, cockroaches and swarm-forming locusts. In each, we discuss the potential effects of the social environment on sensory pathways and sensory-motor integration, as well as on central and neuromodulatory circuits.

Mapping social pathways: opportunities from a neurogenetically accessible model organism

Much of our current understanding of the neural basis of decision-making and behavior comes from research

on the genetically tractable fruit fly, *Drosophila melanogaster*. Despite being previously considered ‘non-social’, *Drosophila* spend a substantial part of their lives surrounded by conspecifics (as well as hetero-specifics), and display a wide range of social behaviors, including odor avoidance [8], collective foraging [9], and social learning [10]. Hence, these flies offer opportunities for mechanistic studies of social behavior. Rearing conditions (including density, degree of relatedness, and strain composition) have prolonged effects on aggression, courtship, partner discrimination, sexual drive and reproduction ([7^{*}] and ref within). As exhibited by many group-living animals, flies pool information that they acquire individually with information gleaned from others ([10–13], and see [14] for larvae). Individuals experiencing conspecifics may potentially be able to make faster and/or more accurate assessment of their environment and gain information that might otherwise not be accessible. Social transmission facilitates collective movement [8], biases mate choice [10,15], triggers change in oviposition site preference [12], and suppresses oviposition rate under potential parasite threats [11].

In all of these cases, individuals are influenced by their surrounding conspecifics via the detection of one or more salient cues related to conspecifics’ behavior. The type of cues detected, and hence the efficiency, time scale, and range of information transfer, can vary considerably. Nevertheless, insights into the neuronal pathways involved suggest that social-based modulation is a broad phenomenon, observed across modalities, circuits, and levels of processing. For example, social facilitation of odor avoidance occurs via a cascade of mechanical inter-fly encounters that elicit directed movement away from the odor zone [8]. Using genetic manipulations for neural silencing and optogenetic activation, it was demonstrated that physical encounters activate the distal leg mechanosensory sensilla neurons and this results in flies moving away from an aversive odor, even when they could not themselves smell it. Social transmission through visual cues [10,15,16] and olfactory cues [12,17] are also common, resulting in behavioral shifts in naïve animals in the presence of experienced ones.

Social cues have been found to be integrated already into primary sensory areas, and hence can have a large impact on behavior. For example, an increased propensity for mating when food is abundant is induced via direct synergistic interactions between pheromone- and food-sensitive projection neurons in the fly antennal lobe (Figure 1b; [18^{**}], and see also in moths, [19]). The coordinated movement of fruit fly larvae results from motion cues from neighboring larvae and spatial visual information being integrated by visual projection neurons [14]. In adult flies the visual projection neurons, LC11, were shown to mediate social transmission of ‘safety’, downregulating freezing behavior when surrounding individuals are moving [16]. The LC11 neurons are sensitive

to the motion of small visual objects, including that of the fly’s surrounding conspecifics, and their activation results in an increased propensity to resume movement after loom-based freezing. A similar effect of ‘safety in numbers’ can be observed across the animal kingdom with evidence that the motion cues provided by surrounding individuals also affect defensive behaviors in mammals, fish, and birds [16]. Within insects, insights into the neural pathways participating in social perception and behavior, as derived from fruit flies, are expected to reveal general principles applicable also to non-model insects that, while less experimentally tractable, nonetheless display different and maybe more complex social attributes, ecology, and behavior.

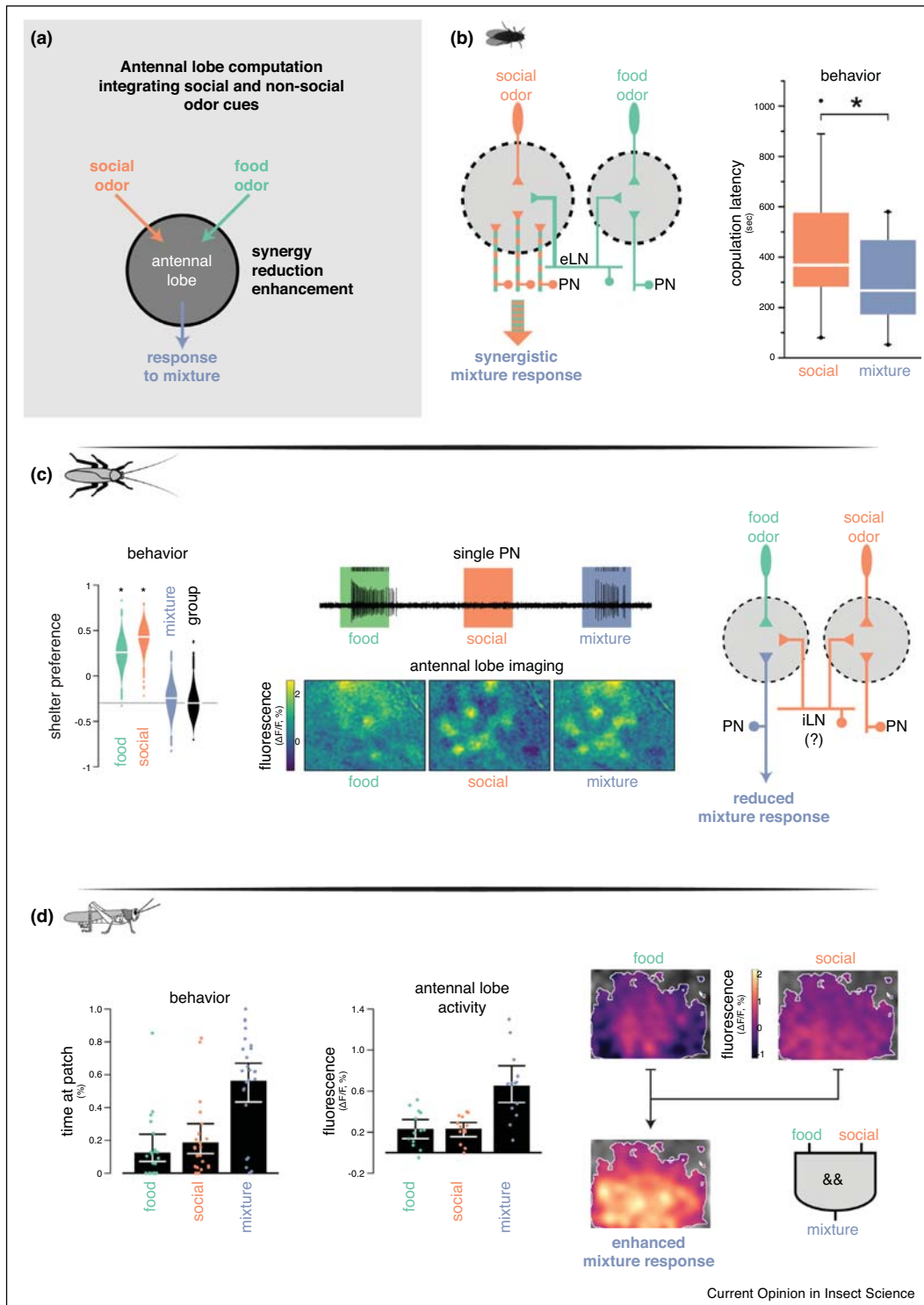
Social facilitation and suppression: lessons from cockroaches

All domiciliary cockroach species reside in aggregations, exhibiting different levels of sociality, with reported evidence of maternal care, chemical communication, kin recognition and central-place foraging [20]. Subsocial species of the wood eating cockroach genus *Cryptocercus* also show altricial development, biparental families and trophallaxis [21]. Being phylogenetically close to the eusocial termites, it was suggested that the cockroaches’ social structure and group dynamics could provide insights into the evolution of both sociality and eusociality.

Cockroaches commonly engage in collective behavior and utilize social information when selecting shelters or food sources, leading to the collective exploitation of a single option amongst multiple alternatives [22^{**},23]. Interestingly, when the available alternatives differ in quality, collective choices can differ from those reached by individual animals alone [24–26]. For example, isolated cockroaches show a clear preference for humid shelters, while in groups they aggregate more under a drier alternative [24]. A similar preference inversion was shown when cockroaches choose between vanillin-shelter (a known attractant to cockroaches, probably associated with food) and an unscented control: when alone, individuals prefer the vanillin shelter; while groups, or when individuals are in the presence of group odor, are more likely to select the control shelter. While still not fully understood, characterization of the shelters’ olfactory representations in the antennal lobe (the first olfactory processing center) suggests a direct interaction between social-sensitive and vanillin-sensitive regions [26] (Figure 1c). Consequently, the vanillin-social odor shelter appears to be evaluated as a distinct olfactory object with an opposite valence, potentially providing a sensory-based mechanism that results in individuals avoiding what they perceive as a recently exploited resource [26].

With increasing group size, social facilitation acts as a positive feedback on cockroach foraging and sheltering

Figure 1



Sensory processing suggests that social and food cues interact in the antennal lobe (AL). **(a)**: A schematic diagram of the integration of social and food odor cues. The final combined output showing synergism, suppression, or facilitation, is based on internal computations between social-related and food-related glomeruli in the AL network. **(b)**: Increased receptivity of virgin female flies to courting males in the presence of vinegar (reduced copulation time: orange versus purple bars) is mediated by electrical synapses between the vinegar-activated excitatory local interneurons and the sex pheromone-responsive projection neurons (modified from [18**]). **(c)**: Change in shelter preference in cockroaches is

behavior as well as on the rate of reproduction and growth [27]. When population density is too high, however, or when a shelter/food site reaches its carrying capacity, crowding results in social suppression [23,28]. To date, however, little is known about the possible neural pathways that mediate this density-dependent switching between social facilitation and suppression.

In relation to colony growth, it has been shown (in *Blattella germanica*) that close-contact social interactions impact juvenile hormone production, regulating the reproductive cycle and hence colony growth, in a density-dependent manner [28]. It is possible that concentration-dependent recruitment of distinct sensory neuron populations may mediate density-dependent reversals, as found in other context-dependent or concentration-dependent behavioral switches (such as in odor preference reversal with increasing stimulus intensity in nematodes, insects, and humans [29]). With current advances in genome sequencing and editing in non-model organisms, cockroaches offer an increasingly appealing model system for mechanistic studies on complex social structures in which an interplay between aggregation and competition takes place.

The social brain of locusts: phase polymorphism and socially induced plasticity

Locust density-dependent phase polyphenism (i.e. the capacity to demonstrate distinct density-dependent phases: solitary, gregarious, and all intermediates), is an extreme example of social-environment-induced plasticity, manifested in a multitude of phase characteristics; but first and foremost it impacts practically all aspects of locust behavior. Much research into the neural basis of locust behavior has, therefore, been aimed at uncovering evidence for phase differences in identified neuronal pathways and structures that may contribute to the well-described phase-specific behaviors [30,31,32*].

The first to be identified and studied were density-induced changes related to sensory perception in different sensory modalities. The responses of receptor neurons in specific types of olfactory sensilla were found to differ between gregarious and solitary desert locusts [33]. Solitary-reared locusts display higher olfactory sensitivity, as this phase possesses a significantly higher number of sensilla and receptor neurons [34,35]. The antennal lobe (AL) of both phases have a similar numbers

of projection neurons; consequently, more receptor neurons converge to each projection neuron in solitary animals, which may account for the differences seen in response specificity, and response profiles between the phases [36].

We have recently characterized the response of the entire population of AL projection neurons in the locust using calcium imaging. The overall response to locust colony odors are strongly reduced in crowd-reared (gregarious) versus solitary animals, reflecting a possible adaptation to a strong crowd-odor background in a high-density social environment (Petelski *et al.*, in prep). In addition, and despite this attenuation, when a colony odor is presented together with a plant extract, the neural responses are strongly enhanced (Figure 1d; Petelski *et al.*, in prep.). This increased neural response is associated with increased attraction to plants where social cues are co-present. These findings suggest that locusts exhibit a social-based sensory modification that enables group foragers to detect food sources that would otherwise be masked by the strong social odors present in dense swarms.

In accord with gregarious insects' more intense flight behavior, the neuronal pathway (interneurons) integrating air-movement stimuli, instrumental for sustaining flight, was reported to be more sensitive in this phase [37]. Plasticity in the visual system was also reported to be correlated with a change in lifestyle of solitary and gregarious locusts including differences in the excitability, and in the habituation, of visual interneurons, as well as in receptive field properties [38,39,40*]. Similarly, changes were also found in the locusts' auditory pathways [41]. These changes in sensory pathways are closely related to a key finding: that the brain regions of gregarious locusts have very different proportions to solitary locusts, and are also 30% larger overall [42].

While providing important insights regarding differences in brain and nervous system-related characteristics that are well suited to the gregarious environment, all the above-described findings fall short of demonstrating direct causal effects of (a change in) the social environment. Geva *et al.* [43] have suggested a learning and memory related mechanism induced by the social cues. Recently, Knebel *et al.* [44**] reported a social-experience-induced internal state, manifested in multiple

observed in the presence of a social odor or in an actual social context (purple and black violins, respectively). Vanillin was used as the food odor and feces extract as the social one. Intracellular recordings from a single vanillin-responsive projection neuron (PN) and calcium imaging from the entire AL, suggest that the activity of vanillin-responsive PNs is suppressed in the presence of a social odor and leads to a change in behavioral preference (calcium imaging, modified from [26]). Right: suggested circuit diagram of interactions between vanillin-responsive and feces-responsive glomeruli (d): Both food and social cues are required for an approach to take place in locusts. Behavioral experiments (left panel) show that social feedback strongly impacts food patch selection. Calcium imaging from a large population of PNs in the AL shows weak responses to the food odor (green leaves) and the colony odor, and a significantly stronger response when both are presented together. In both behavior and AL activity panels, bars show population average and single dots are corresponding individual animals. The observations suggest an AL computation of a strong response facilitation or an 'and gate' (from Petelski *et al.*, in prep).

aspects of locust walking and marching behavior kinematics. This state of the individual is directly induced by the experience of collective motion within a locust swarm. On the one hand, this finding reflects earlier findings regarding the motor control of posture [45], while on the other hand also being strongly related to sensory processing (of social-environment-related stimuli) and sensory-motor integration. The underlying neuronal mechanisms are yet to be described.

Concluding remarks — cross species analysis and open questions

Here we have presented a short overview of current advances in our understanding of the neural substrate involved in regulating social behavior in non-eusocial insects. Detailed neuronal pathways, dissected in the genetically accessible fruit fly, well align with findings from cockroaches, which exhibit more complex social structures, and also with those from locusts, which provide a unique opportunity to study adaptations to a solitary and gregarious lifestyle in a single species. These species have been shown to share common principles of how social cues are integrated in primary sensory areas, and consequently, how they can have a broad impact on behavioral choices (Figure 1), highlighting the ecological importance of the social environment.

The ‘social brain hypothesis’ was posited as an evolutionary explanation for certain unique morphological characteristics of the brain (e.g. substantially enlarged brains) of social mammals, driven by the cognitive demands of sociality. Lihoreau *et al.* [46] argue that in order to understand how animal behavior and cognition are shaped by the environment (including the social interactions), one should focus on brain functions and seek to identify the neural circuitry correlates of social tasks. In some insect lineages, however, the acquisition of an enlarged integration center predates the appearance of social traits, and is thus more likely to have been driven by selection for other sensory and ecological challenges, such as an increase in home range that requires a more sophisticated spatial memory, multisensory integration, and spatial learning [4]. Furthermore, many examples indicate that cognitive capacities are not always manifested in volumetric brain changes, and that other cellular and subcellular traits, expressing variation across closely related species with different social characteristics, may serve as more robust variables for evolutionary analysis [6].

When focusing on social perception and behavior, a major question arises regarding what differentiates the social environment from other complex environmental features. On the neural level this translates to two-specific questions: (1) How do the perception and interpretation of social cues differ from those of other sensory inputs; (2)

Do social interactions require distinct cognitive processes? These are by and large still open questions [46,6] that can and should be discussed in light of the recent developments in mapping the neural circuits involved in social processing, as described herein.

In terms of perception, sensory systems are tuned to salient cues in the environment, which in the case of social stimuli include the current and/or previous presence, and in some cases also the behavior, of conspecifics. Different sensory modalities reveal different levels of specialization in the way by which social cues are detected and interpreted: from specialized olfactory structures (e.g. pheromone-specific sensilla innervating a separate population of projection neurons), to generalized pathways in other sensory modalities, capturing both social and non-social stimuli. In the latter case, social cues can nonetheless be discriminated from other stimuli based on their particular features (i.e. certain objects’ shape/size/coloration or motion in vision stimuli, or certain frequency/intensity bands in tactile or auditory stimuli). The evolution of specific mechanisms dedicated to social cues may have long reaching effects on different aspects of the organism’s ecology (and even lead to ecological divergence [47]).

In many of the examples presented here, as also observed in other organisms (e.g. Ref. [48]), individuals demonstrate a high sensitivity to particular features of the movement/appearance of conspecifics that is sufficient to induce social-related changes in behavior. Visual projection neurons sensitive to the motion of small objects, or tactile antennal receptors sensitive to conspecifics or heterospecifics, suggests the existence of overlapping pathways for capturing both social and asocial stimuli at primary sensory levels. It is likely, however, that in higher brain regions, distinct neuronal populations specialize in the classification, processing and selection of distinct social-related behavioral outputs. A promising candidate for a social specific module is that of the mushroom body’s γ lobe, which encodes social experiences in honey bees [49••] and social attraction in fruit flies [50•]. As more such examples will be described, and from more and different species, greater insights will be obtained into understanding the interactions between insects and their social environment, and perhaps also into the evolution of the social brain.

Conflict of interest statement

Nothing declared.

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