Information transfer beyond the waggle dance: observational learning in bees and flies

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Social information transfer is part of the success of animal societies and has been documented in a variety of taxa, from slime molds to humans. In invertebrates, the historical research focus has been on the specialized signals shaped by selection to convey information, such as the honeybee waggle dance. However, growing evidence shows that invertebrates also commonly glean critical information about their environment by observing others. For instance, a bumblebee's choice between novel flower species is influenced by the observation of the foraging choices of more experienced conspecifics. Recent studies suggest that these seemingly complex learning abilities can be explained in terms of simple associative learning, whereby individuals learn to associate social cues (conditioned stimuli) to reward cues (unconditioned stimuli). Here, we review the behavioral evidence of observational learning both in bees and *Drosophila*. We discuss the validity of associative accounts of observational learning and the potential neural circuits mediating visual social learning in these model species to define future research avenues for studying the neurobiology of social cognition in miniature brains.

Keywords: bumblebees, *Drosophila*, social cognition, social learning, visual cognition

Introduction

The waggle dance of the honey bee constitutes one of the most sophisticated systems known for information transfer about profitable food sources (Von Frisch, 1967). A successful forager performs a stereotyped behavior within the hive, originally described as a "dance," which conveys information about the direction and distance from the hive of an exploited food source (Riley et al., 2005; Grüter and Farina, 2009; Seeley, 2010). This dance "language" is a case of true communication (Markl, 1985) whereby the sender explicitly transfers information to the receivers in order to modify their behavior. Yet, many animals use social information to learn about their environment simply by attending the behavior of others (Danchin et al., 2004; Galef and Laland, 2005). This type of social learning differs from true communication in that the demonstrator does not explicitly attempt to modify the receiver's behavior. In this review we will focus on social learning based on visual observation of a demonstrator's behavior (Zentall, 2012).

Invertebrates provide paradigmatic examples of observational learning. For instance, *Octopus* observers that are allowed to watch conditioned *Octopus* demonstrators choosing one of two different colored objects presented simultaneously, consistently select the

same object as the demonstrators did (Fiorito and Scotto, 1992). Other fascinating cases are found among insects. These animals exhibit developed learning capacities and accessible miniature nervous systems, thereby constituting ideal organisms for dissecting the neural and molecular bases of learning (Giurfa, 2013). Model species, such as the honey bee *Apis mellifera* (Menzel, 1999; Giurfa, 2007; Galizia et al., 2012), and the fruit fly *Drosophila melanogaster* (Heisenberg, 2003; Davis, 2005; Guven-Ozkan and Davis, 2014) have been extremely useful for pioneer studies on the mechanisms of learning and memory.

Here we focus on social bees (Hymenoptera) and *Drosophila*, in which observational learning has been documented. Our goal, beyond various excellent reviews on the topic of social learning in insects (e.g., Leadbeater and Chittka, 2007b; Dukas, 2008; Grüter and Leadbeater, 2014; Leadbeater, 2015) is to provide a mechanistic view of these complex behaviors. It has recently been suggested that social learning can emerge from simple associations between a relevant stimulus (unconditioned stimulus, US), such as a food reward or a predator threat, and a conspecific's presence or behavior (conditioned stimulus, CS), which is not different from individual learning of non-social cues (Leadbeater and Chittka, 2007b; Avarguès-Weber et al., 2011; Heyes, 2011; Giurfa, 2012). Using this idea, we discuss the nature of learning associations and the neural circuits potentially involved in insect observational learning.

Observational Learning in Bees

Behavioral Evidences

During their foraging activities, bees need to exploit multiple floral resources whose reward levels change rapidly and unpredictably (Heinrich, 1979, 2004; Goulson, 2010; Lihoreau et al., 2012b). A forager's choice of plant species is guided by unlearned preferences and learned information about current reward levels gained through individual sampling (Raine et al., 2006). As many pollinators often work concurrently in a meadow, information acquired individually can be complemented by social information (Grüter and Leadbeater, 2014), but also by information gained inside the nest through communication and food exchange (Biesmeijer and Seeley, 2005; Arenas et al., 2008). It has long been known that during foraging, bees are attracted to visibly occupied flowers [e.g., bumblebees (Brian, 1957); stingless bees (Slaa et al., 2003); honey bees (Von Frisch, 1967), suggesting that they learn to exploit food resources by copying the choices of other bees (Romanes, 1884)]. Recent studies with bumblebees have shown that individuals can indeed glean information from watching other foragers, and change accordingly their floral choices (Leadbeater and Chittka, 2005, 2007a; Worden and Papaj, 2005; Kawaguchi et al., 2007; Baude et al., 2011; Avarguès-Weber and Chittka, 2014a,b), their choice of location (Leadbeater and Chittka, 2005, 2009; Kawaguchi et al., 2006; Baude et al., 2008; Dawson and Chittka, 2012; Plowright et al., 2013) and their handling strategies (Leadbeater and Chittka, 2008; Goulson et al., 2013; Mirwan and Kevan, 2013).

In particular, when bees observe the floral choices of conspecific demonstrators from behind a transparent screen (**Figure 1A**), they land more often on the flower type chosen
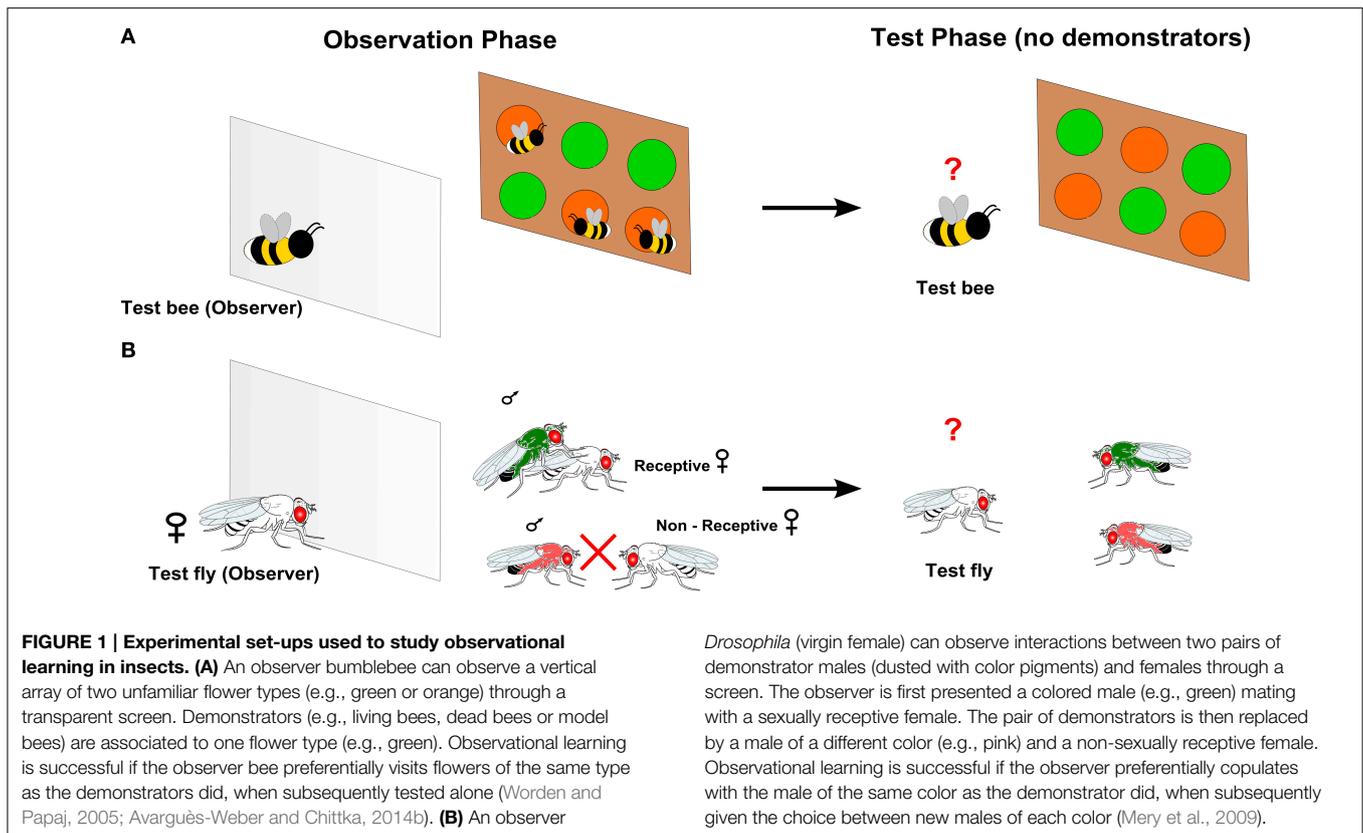
by demonstrators in tests where the demonstrators are absent, than compared to non-observing controls (conspecifics separated from demonstrators by an opaque screen) (Worden and Papaj, 2005). Similar results are obtained with artificial demonstrators (inanimate model bees made of resin), thus indicating that visual cues associated with the presence of conspecifics are sufficient to promote social acquisition of flower preferences (Worden and Papaj, 2005; Dawson et al., 2013; Avarguès-Weber and Chittka, 2014b).

An Associative Account

The fact that bees acquire flower preferences by observing foragers through a screen (Worden and Papaj, 2005; Dawson et al., 2013; Avarguès-Weber and Chittka, 2014b) is incompatible with a simple associative hypothesis in which foragers associate profitable flowers (US) with the presence of the conspecifics (CS). In this case, the demonstrators are no longer present when the observer makes its choice, which implies that the positive value of conspecifics has been transferred to the associated flowers themselves. An explanation based on associative learning is still possible but in the form of a phenomenon termed second-order conditioning (Pavlov, 1927). Under second-order conditioning, bees learn a positive association between a conspecific (CS1) and a food reward (US), due to past-shared foraging experience on the same resources. When observing a conspecific feeding from an unknown flower, the close association between the CS1 (conspecifics) and the flower induces the bee to consider flower cues themselves as indicative of reward (CS2). Such a mechanism would lead to a socially acquired preference for all flowers sharing the same characteristics and not only for the occupied flowers (Leadbeater and Chittka, 2007b; Dawson et al., 2013).

If observational learning for new flower preferences is the consequence of a second-order conditioning, then impeding or modifying the first association should alter flower preference. In bumblebees, this hypothesis is supported by the fact that naive bees with no previous social foraging experience tend to ignore the choices of conspecifics in their foraging decision (Dawson et al., 2013; Avarguès-Weber and Chittka, 2014a), suggesting that there is a decisive role of prior associations between social cues and a reward. Additionally, the preference for socially demonstrated flowers can be reversed into avoidance if the tested bees are allowed to form an association between the conspecifics and a bitter aversive solution beforehand (Dawson et al., 2013).

The associative learning hypothesis also predicts that non-social cues should promote social-like learning behavior given that they have been previously associated with rewarding flowers. However, bumblebees follow different flower choice strategies when social cues (model bees) or non-social cues (wooden white blocks) are used as indicators of reward (Avarguès-Weber and Chittka, 2014a). If they have learned that the white blocks are present on a rewarded flower color, they will choose afterwards a different color, only if it displays the presence of the blocks. Unoccupied flowers presenting that same color will not be chosen. This behavior can be explained in simple associative terms as the blocks were previously associated with reward. The situation is different if bees have learned to forage on a flower color on which bees were present. In this case, they will choose afterwards a novel

FIGURE 1 | Experimental set-ups used to study observational learning in insects. (A) An observer bumblebee can observe a vertical array of two unfamiliar flower types (e.g., green or orange) through a transparent screen. Demonstrators (e.g., living bees, dead bees or model bees) are associated to one flower type (e.g., green). Observational learning is successful if the observer bee preferentially visits flowers of the same type as the demonstrators did, when subsequently tested alone (Worden and Papaj, 2005; Avarguès-Weber and Chittka, 2014b). **(B)** An observer *Drosophila* (virgin female) can observe interactions between two pairs of demonstrator males (dusted with color pigments) and females through a screen. The observer is first presented a colored male (e.g., green) mating with a sexually receptive female. The pair of demonstrators is then replaced by a male of a different color (e.g., pink) and a non-sexually receptive female. Observational learning is successful if the observer preferentially copulates with the male of the same color as the demonstrator did, when subsequently given the choice between new males of each color (Mery et al., 2009).

color if dummy bees are present on it but, in addition, they will extend their choice to unoccupied flowers with that same color. Thus, in the latter case, the bees' choice is not restricted to the flowers occupied by a model bee but includes all flowers presenting the same characteristics (Avarguès-Weber and Chittka, 2014a). The difference between these two scenarios may reside in the fact that foragers gather experience in the field in which conspecifics, contrary to wooden blocks, are not only predictive of reward but also mobile. This mobility may allow transferring the choice form the occupied flower to the unoccupied flower as long as both share the same color. This strategy may be advantageous: in many typical flower species, it might not be adaptive for a pollinator to visit a flower that is currently being drained by another visitor. Instead, it would be more useful to steer toward unvisited flowers of the same plant species where the visitation activities of others indicate that the flower type is profitable. Therefore, specific mechanisms might have evolved to promote efficient social information use in flower foraging, suggesting that social and asocial learning are dissociated.

It is, however, also possible that there is no special role of conspecifics in the flower generalization pattern observed, specifically when demonstrators indicate rewarding flowers. Bees that never got the chance to see live conspecifics within or outside the nest and were only familiarized with model static bees pinned on flowers show a pattern of choices similar to that of bees familiarized and tested with non-social cues (Avarguès-Weber and Chittka, 2014a). By contrast, bees exposed to live bees experienced that the socially indicated flower species will sometimes be occupied by demonstrators and sometimes not, occasionally in rapid succession, and the situation might change while the observer is on the flower. Thus, observers will get exposure to mobile demonstrators physically dissociated from the flowers, and this in turn may favor future generalization to unoccupied but socially indicated flowers. The possibility that non-social moving objects could generate a social-like flower choice pattern remains to be tested. Alternatively, social learning specificity may require a familiarization phase with live conspecifics to learn to associate the conspecific's chemical signature acquired within the nest (Krasnec and Breed, 2012), and with the species visual characteristics.

Relying on the choices of others is not always an adaptive strategy (Giraldeau et al., 2002; Laland, 2004; Rieucau and Giraldeau, 2011; Grüter and Leadbeater, 2014). In the most extreme case of a population always favoring social learning over individual sampling, an ecological dead end would be quickly reached with some resources being overexploited while others are left unexplored. From the colony perspective, keeping enough individual information acquisition is essential for social learning behavior to remain beneficial (Giraldeau et al., 2002; Rieucau and Giraldeau, 2011; Grüter and Leadbeater, 2014). Bumblebees present restrictions in the use of social over individual learning that are consistent with the theory. Indeed, the response to social cues is flexible, depending on the context of the observation (Leadbeater and Chittka, 2005; Kawaguchi et al., 2007; Baude et al., 2011). In a

field study, *B. diversus* foragers were given a choice between two inflorescences attached to a stick ("interview bouquet"), one of which was occupied by a conspecific (freshly killed bee pinned on flowers). While bees preferred occupied inflorescences when they were presented two unfamiliar flower species, they avoided conspecifics when confronted with flower species found in their daily environment (Kawaguchi et al., 2007). Presumably, this conditional use of social information enables bees to maximize their foraging efficiency when searching for novel food items while minimizing the costs of competition when they know resource locations (Laland, 2004; Dall et al., 2005). Competition level is also reduced by another flexible usage of social information as *B. terrestris* foragers do not follow the preferences of demonstrators when the conspecifics density on the flowers patch is too high (Baude et al., 2011; Plowright et al., 2013).

All these results suggest that observational social learning in bumblebees is the consequence of simple associative processes and specific enhanced attention toward conspecifics as cue providers (stimulus enhancement) and/or places where these conspecifics can be seen (local enhancement) (Zentall, 2006; Leadbeater, 2015). An intricate interplay between evolutionary adaptation to attend to conspecific cues, individual experience with such cues and their contingencies with salient aspects of the environment is probably at hand to generate the observed complexity of observational social learning.

Observational Learning in *Drosophila*

Behavioral Evidence
Although considerable knowledge on insect observational learning comes from research on bumblebees, visual social learning has also been described in a non-social species, the fruit fly *D. melanogaster*. In this species, females learn the quality of potential mating partners by observing their success with other females (Mery et al., 2009) (**Figure 1B**). This capacity was shown in experiments in which two artificial male phenotypes were produced by dusting flies with green or pink pigments (Mery et al., 2009). An observer (virgin) female was placed in a glass tube where she could see demonstrator males and females through a colorless screen. In the first observation phase, the demonstrator male (e.g., green) successfully mated with the demonstrator female. In the second phase, a male of another color (e.g., pink) was paired with a non-receptive female, thus leading to unsuccessful copulation attempts by the male. When the observer female was later presented with two males (green and pink) simultaneously, she preferentially mated with the male of the color that was associated with a successful copulation (e.g., green) (**Figure 1B**). This effect disappeared when the observers could not directly observe the demonstrator flies (Mery et al., 2009). This example shows that observational learning is not restricted to social insects. Rather, it seems to be a general capacity issued from the insects' faculty to learn associations in their environment. Observational learning in *Drosophila* could also be interpreted as a special case of associative visual learning. It is possible that the vision of a female copulating with a male acts as a biologically relevant reinforcement to be associated with the male color (CS). Under this hypothe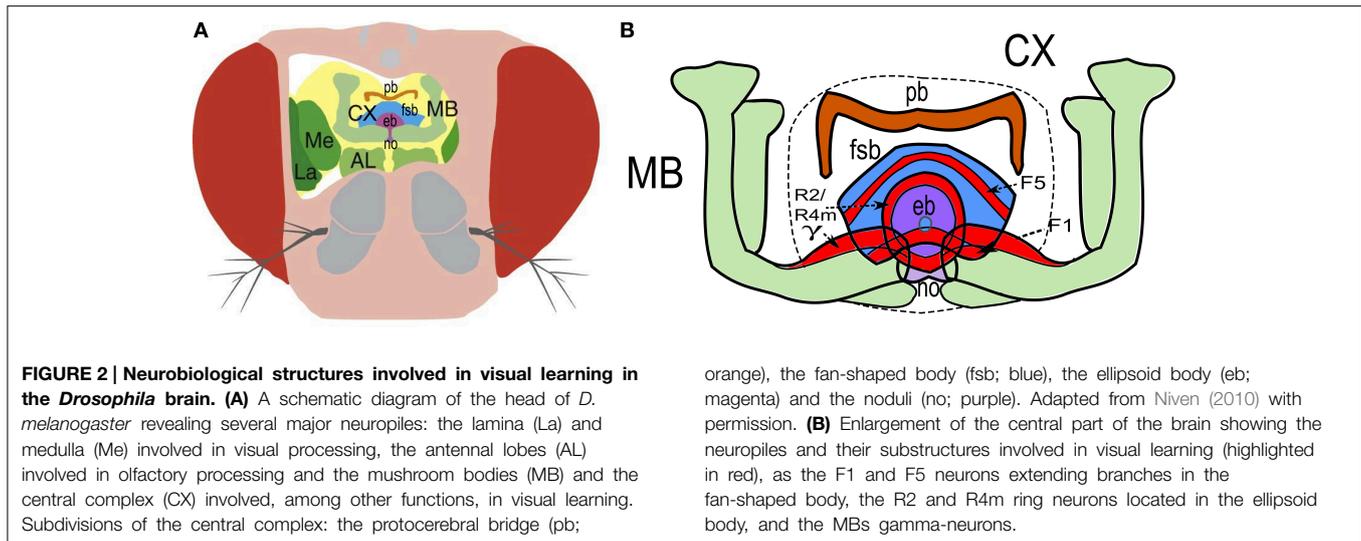sis, observer flies should learn to associate a male color phenotype with a successful mating signal. Later, when confronted with males of different phenotypes, observers would preferentially choose the learned color based on a simple associative memory. Visual associative learning has been extensively documented in *Drosophila* in an individual context (Heisenberg et al., 2001; Foucaud et al., 2010; Schnaitmann et al., 2010; Ofstad et al., 2011; Vogt et al., 2014) so that transferring this capacity to a mating, observational context is plausible.

Genetic and Molecular Basis
The discovery of mate choice copying in a main model organism holds considerable promises to unravel the genetic and molecular substrates of observational learning in insects, an approach that is currently not possible in bees. While such analysis has not been conducted yet, recent studies have begun to identify the neural substrates of *Drosophila* visual learning that may also be involved in observational learning in particular if the associative learning hypothesis is verified.

Different forms of visual learning are mediated by the central complex (CX). This neuropil is located between the protocerebral brain hemispheres and comprises four interconnected regions: the fan-shaped body, the ellipsoid body, the protocerebral bridge and the paired noduli (**Figure 2**). It receives information from visual processing neuropils (lamina, lobula, medulla) connected to each compound eye, and whose learning-dependent plasticity has not been explored until now. The implication of the CX in visual recognition was first demonstrated using a flight simulator, in which a fly whose head is attached to a torque meter controls the position of visual patterns on the walls of a circular arena with its flight direction (Heisenberg et al., 2001). Using this approach, flies can be trained to learn to avoid visual cues (such as colors and geometric forms, CS) due to their association with an aversive stimulus (a heat beam, US). The sequence of CS and US stimuli can either be controlled by the fly itself (operant training) or by the experimenter (Pavlovian training) (Brembs and Heisenberg, 2000). Memory mutants lacking the Rutabaga (Rut) protein—a type 1 Ca2+/Calmodulin-dependent adenylyl cyclase that produces cAMP—display impaired operant and Pavlovian visual learning, indicating that Rut plays a decisive role in the US/CS association, probably as a coincidence detector of the visual CS and the heat US (Liu et al., 2006). By using the UAS/GAL4 system to differentially express Rut in specific subsets of cerebral neurons, it has been shown that the discrimination of visual patterns of different elevations or orientations requires two different groups of neurons extending branches in the fan-shaped body, respectively the F5 and F1 neurons (Liu et al., 2006). Another subset of large field neurons located in the ellipsoid body (the ring neurons R2 and R4m) are also involved in recognition of several pattern features through excitatory and inhibitory visual subfields (Pan et al., 2009; Seelig and Jayaraman, 2013) (**Figure 2**). Taken together, these results demonstrate the implication of the CX in visual learning and memory through dynamic interactions between the ellipsoid-body and the fan-shaped body.

Recent studies also point toward a contribution of the mushroom bodies (MBs) in visual memories. The MBs are central brain structures involved in olfactory learning and

FIGURE 2 | Neurobiological structures involved in visual learning in the *Drosophila* brain. (A) A schematic diagram of the head of *D. melanogaster* revealing several major neuropiles: the lamina (La) and medulla (Me) involved in visual processing, the antennal lobes (AL) involved in olfactory processing and the mushroom bodies (MB) and the central complex (CX) involved, among other functions, in visual learning. Subdivisions of the central complex: the protocerebral bridge (pb; orange), the fan-shaped body (fsb; blue), the ellipsoid body (eb; magenta) and the noduli (no; purple). Adapted from Niven (2010) with permission. **(B)** Enlargement of the central part of the brain showing the neuropiles and their substructures involved in visual learning (highlighted in red), as the F1 and F5 neurons extending branches in the fan-shaped body, the R2 and R4m ring neurons located in the ellipsoid body, and the MBs gamma-neurons.

memory (Davis, 2005), courtship (McBride et al., 1999), locomotion (Martin et al., 1998), and sleep (Joiner et al., 2006; Pitman et al., 2006), among others. Despite the absence of obvious anatomical connections between the optic lobes to the MBs (Barth and Heisenberg, 1997; Otsuna and Ito, 2006; Mu et al., 2012), the volume of the MB calyces (dendrites) changes with light regime, suggesting that MBs are involved in visual information processing (Barth and Heisenberg, 1997). Indeed, it has been shown that MBs are required in visual context generalization (Liu et al., 1999) and could stabilize visual memories against context changes (Brembs and Wiener, 2006). Interestingly, the MBs (γ neurons) seem also necessary for the memorization of simple associations between color stimuli and a sugar reward or with an electric shock (Vogt et al., 2014). Presumably, the implication of the CX or the MBs might be dependent of the locomotion state (flying vs. walking) as flies were trained in a flight simulator in one case (Liu et al., 2006; Pan et al., 2009) vs. a walking plate in the other (Vogt et al., 2014). Locomotor activity is known to affect the activity of octopamine neurons and the behavioral response to CO_2 (Suver et al., 2012; Wasserman et al., 2013), and thus possibly modifies neural pathways involved in visual information memorization (Kottler and Van Swinderen, 2014; Vogt et al., 2014). Additionally, walking activity has no direct effect on the activity of ring neurons of the CX while flying activity significantly decreases their responses to visual stimuli (Seelig and Jayaraman, 2013).

Importantly, the MBs and their associate dopaminergic signaling are also involved in visual attention in the form of visual tracking of a moving bar (Xi et al., 2008; Van Swinderen et al., 2009). They may consequently mediate the specific attentional state elicited by social visual cues during an observational learning task.

Conclusion

Placing social learning within the conceptual framework of associative learning is an appealing approach for explaining seemingly complex behavior in insects with pinhead-sized brains. However, bumblebee studies are beginning to suggest that observational learning by insects does not only reflect visual associative learning but also involves attentional processing of social cues as information providers.

In parallel, the neurogenetic approaches well mastered in *Drosophila* hold considerable promises in revealing the neural basis of such complex behavior. Future investigations may target the CX and MBs as the potential neuronal structures involved, given their implication in visual learning and attention.

The popularity of bees and fruit flies as models for visual cognition research associated with the abundance of genomic information available make them ideal study systems to explore the genetic, molecular, neuronal, and behavioral basis of visual social learning, a major challenge on the way of understanding the evolutionary relationships between animal brains, cognitive capacities and their social environment (Lihoreau et al., 2012a).

Acknowledgments

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