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Multisensory integration of colors and scents: insights from bees and flowers

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Abstract Karl von Frisch's studies of bees' color vision and chemical senses opened a window into the perceptual world of a species other than our own. A century of subsequent research on bees' visual and olfactory systems has developed along two productive but independent trajectories, leaving the questions of how and why bees use these two senses in concert largely unexplored. Given current interest in multimodal communication and recently discovered interplay between olfaction and vision in humans and *Drosophila*, understanding multisensory integration in bees is an opportunity to advance knowledge across fields. Using a classic ethological framework, we formulate proximate and ultimate perspectives on bees' use of multisensory stimuli. We discuss interactions between scent and color in the context of bee cognition and perception, focusing on mechanistic and functional approaches, and we highlight opportunities to further explore the development and evolution of multisensory integration. We argue that although the visual and olfactory worlds of bees are perhaps the best-studied of any non-human species, research focusing on the interactions between these two sensory modalities is vitally needed.

Keywords Multimodal · Bees · Integration · Color · Scent

Abbreviations

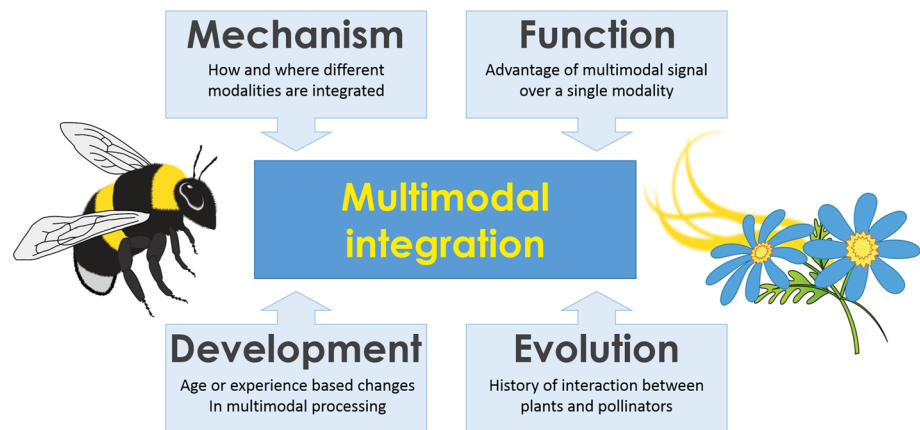
AL Antennal lobe
KC Kenyon cell
MB Mushroom body
PER Proboscis extension response

When Karl von Frisch first began his studies of honeybees at the beginning of the last century, it was not clear that bees perceived either color or scent. Reflecting upon a claim of contemporary researchers that bees were color-blind, he observed that “once one got to know, through work in the field, something about the reaction of bees to the brilliant colour of flowers, it was easier to believe that a scientist had come to a false conclusion than that Nature had made an absurd mistake” (von Frisch 1966). A century later, bees' visual and olfactory processing systems continue to be the “magic well” von Frisch predicted (Giurfa 2007), inspiring research programs in behavioral neuroscience, signal evolution, and sensory ecology. Thanks to von Frisch's role as a popularizer of this knowledge (e.g. von Frisch 1956), the general public may know more about the multisensory worlds of bees than any other animal, from the well-known presence of hidden UV patterns on flowers to the chemical detection capabilities of modern “bomb sniffing” bees (Rodacy et al. 2002).

In light of von Frisch's famous comment, the centennial of his work offers an occasion to examine other disconnects between how we often study bees and their observed interactions with the natural world. For example, while vision and olfaction are the two senses studied most widely in bees, they may also be the two senses studied most independently from each other. None would argue that a bee flying through a flower-filled meadow experiences a world of “scentless” colors or “colorless” scents, but most experiments, rather than involving multisensory stimuli, focus exclusively on vision or olfaction. Indeed, only about 5 % of journal articles on bee learning from the past 20 years explicitly consider bees' responses to multimodal stimuli (Leonard et al. 2012). During this period, interest in understanding how and why animals respond to multimodal signals has surged among behavioral biologists (Partan and

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Fig. 1 Tinbergen's questions applied to the integration of floral colors and scents. This framework suggests four complimentary perspectives on understanding how and why pollinators use multimodal stimuli



Marler 1999; Rowe 1999; Hebets and Papaj 2005), generating a number of recent conference symposia and special issues (e.g. Hebets 2011; Partan 2013). Likewise, neuroscientists have uncovered intriguing perceptual cross-talk between olfaction and vision in humans and *Drosophila* (e.g. Small 2004; Stewart et al. 2010). In each of these fields, a historical focus on studying sensory modalities independently has led to major gaps in our understanding of the evolution of complex communication (Coleman 2009) and the workings of the perceptual brain (Alais et al. 2010; Bremner et al. 2012).

With so many open questions, few other systems can compete with bees' potential as holistic models of multisensory processing. A century of research on vision and olfaction has generated a wealth of neuroanatomical insights, experimental protocols, and perceptual models (rev. Menzel 1983; Chittka and Raine 2006). Further, in contrast to other model systems (e.g. *Drosophila*), bees are uniquely positioned to advance understanding of multisensory integration because the colors and scents relevant in a foraging context are the products of coevolution with their plant producers. As signals, they face selection not only from the physical environment, but also from the sensory and nervous systems of receivers (Guilford and Dawkins 1993). Thus, we have the potential to consider what we learn about how bees integrate stimuli in both evolutionary and ecological contexts. We can ask how multisensory aspects of floral displays have evolved to manipulate bee behavior (Raguso 2004; Schaefer et al. 2004; Schaefer and Ruxton 2010); likewise, we can ask whether the perceptual systems of bees may have evolved to manage complex multimodal floral stimuli. The stage is thus set for innovative research into multisensory processing, from both proximate and ultimate perspectives.

Here we review what is currently known about how bees integrate multimodal floral stimuli. We define multisensory integration as "the set of processes by which information arriving from the individual sensory modalities (e.g. vision,

audition, touch) interacts and influences processing in other sensory modalities, including how these sensory inputs are combined together to yield a unified perceptual experience of multisensory events" (Talsma et al. 2010). We focus nearly exclusively on scent and color although bees certainly respond to further intra-modal complexity (rev. Dafni et al. 1997; Raguso 2008) and integrate stimuli from additional sensory modalities (e.g. taste and touch or touch and smell—areas of particular interest to von Frisch). Our perspective is receiver-focused; for a framework of functional hypotheses for complex floral displays (i.e. the complimentary "plant's eye-view") we direct readers to other recent reviews (Leonard et al. 2011a, 2012). Although our focus is on bees' response to floral signals, we draw on findings related to multisensory integration in other systems (humans, *Drosophila*, and hawkmoths). This review is not exhaustive; rather, we suggest a framework for organizing thinking about multisensory integration, with the hope that it may spur research at the interface of additional modalities, revealing unexplored territory in the bee's perceptual world.

This framework (Fig. 1) is based on the template of another foundational ethologist and von Frisch's Nobel co-recipient, Nikolaas Tinbergen. In his classic paper, Tinbergen (1963) suggested organizing the study of behavior according to four questions: (1) causation (mechanism), (2) ontogeny (development), (3) survival value (function), and (4) evolutionary history. This structure allows behavioral biologists to clearly align alternative hypotheses at appropriate levels of analysis. While a mechanistic perspective on multisensory integration may be most familiar, far less is known about how bees actually benefit by using multisensory stimuli (function). In the cases of ontogeny and evolution, we are at a point of formulating questions rather than cataloging answers. Applying Tinbergen's four questions to multisensory integration highlights the interdisciplinary potential of this research program, as it brings together insights from animal communication, neuroscience, cognitive ecology, and pollination biology.

Mechanisms of multisensory integration

To fully consider the mechanisms of multisensory integration, we would eventually like to map the neural pathways involved, understand how olfaction and vision work together to control behavior, and then ask how those behavioral processes play out in ecologically relevant foraging contexts. A full picture of how bees use both senses in concert will ultimately require insights from neuroethology, cognitive psychology, and sensory ecology.

Neural mechanisms

Many questions remain about multimodal integration and cross-modal modulation at the neuronal level. The integration or modulation of multimodal sensory inputs might happen at a peripheral level, at the output neurons converging to final behavior, or at any intermediate point along the processing path. In light of these possibilities, it is clear that localization of the neuronal mechanism(s) underlying multimodal processing is not an easy task. Moreover, it is possible that multimodal integration does not always happen at the same place (Erber 1978).

At least in bees, the mushroom bodies (MBs) are widely viewed as the major sites of multisensory integration, in addition to playing a major role in learning, memory, and motor control (Menzel 1999; Heisenberg 2003; Strausfeld 2012). MBs consist of tightly packed parallel-running bundles of axons that usually bifurcate into two lobes. These intrinsic neurons (Kenyon cells—KCs) are organized in several subsystems that reflect compartmentalization of neuronal inputs of different modalities and/or different forms of memories (Strausfeld 2002; Strausfeld et al. 2009). The dendritic side often forms an elaborate structure called a calyx, which allows access to a multitude of input neurons. The complexity of the calyx is thought to be correlated with the richness of sensory input into MBs (Farris 2013). In hymenopterans, these structures receive input from pathways related to the processing of both olfactory information (from antennal lobes, AL) and visual information (from optic lobes). The lip receives olfactory input from ALs, the basal ring receives input from olfactory projection neurons and from visual neurons from the medulla (Gronenberg 1999). The collar ring receives both visual and olfactory input as collaterals of the same neurons (Mobbs 1982; Gronenberg 2001; Ehmer and Gronenberg 2002). In addition, certain KCs integrate across all the regions of MBs calyces, allowing inputs from the olfactory as well as from the visual system (Strausfeld 2002). Electrophysiological recordings of honeybee MB interneurons support their putative role in multisensory integration (Erber 1978).

The MBs have been repeatedly shown to be the site of olfactory memory formation (Menzel 2001; Gerber et al.

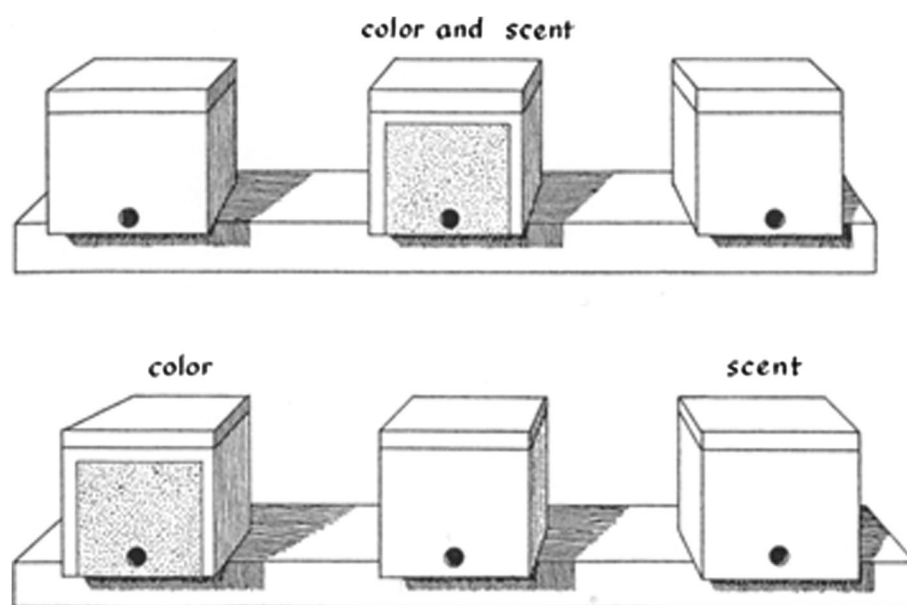
2004; Davis 2005), but some forms of olfactory memories have been also assigned to synaptic changes in the antennal lobes (Yu et al. 2004; Galán et al. 2006). On the contrary, studies in *Drosophila* have shown that visual memory traces mediating visual pattern recognition are stored in another central neuropile of the fly brain, the fan-shaped body (Liu et al. 2006) and visual place learning is localized into the ellipsoid body (Ofstad et al. 2011). In flies, simple visual, tactile and motor memories are independent of MBs and only the visual context associated with memory formation is MB-dependent (Wolf et al. 1998; Liu et al. 1999).

Functional feedback from the MBs to the ALs interneurons and projection neurons has been described in bees as well as in flies (Rybak and Menzel 1993; Hu et al. 2010), yet from different regions of MBs. This suggests that either this feedback is species-specific or, more likely, that there are multiple feedbacks from KCs regulating response to olfactory stimuli. In bees, calyces receive multiple feedback neurons originating in the lobes but there is no simple within-modality arrangement. Inhibitory neurons also originating in KCs are supplied by olfactory projection neurons innervating parts of the calyx that receive visual input and vice versa (Grünewald 1999). This arrangement supports the notion that encoding and processing of one modality depends on feedback from the other modality.

Cognitive mechanisms

The question of how bees form associations between scents, colors, and rewards involves fundamental questions about elemental and non-elemental processes in learning (Giurfa 2003, 2007; Balkenius et al. 2008; Young et al. 2011). During elemental learning, the bee forms an association between a stimulus and a reinforcer (e.g. Scent₁/Color₁+, absolute conditioning) or absence of reinforcer (e.g. Scent₁/Color₁+ vs. Scent₂/Color₂−, differential conditioning); importantly, each component of the rewarded stimulus is always unambiguously associated with reward. Using an elemental strategy, a bee would be expected to learn a color-scent compound as the sum of its parts and thus, in principle, to respond to both the color and scent presented in isolation. In practice, visual and olfactory components of a bimodal compound may hold different associative strength for bees. In an early series of experiments, Couvillon and Bitterman (1980, 1982) trained free-flying honeybees to associate a sucrose reward with a bimodal compound stimulus and then compared their responses to a panel of unimodal or bimodal stimuli. They found that scent overshadowed color: bees trained to a compound of scent and color later responded less to color alone than did bees trained only to color. This finding mirrors an earlier result of von Frisch's (Fig. 2): after keeping a honeybee colony in a box paired with a distinct combination

Fig. 2 Scheme used by von Frisch to assess honeybee foragers' reliance on color vs. scent in colony identification. Bees were kept in the central colony box characterized by a color–scent combination (*top row*) and offered a choice between boxes with either the familiar scent or color (*bottom row*). Reprinted from Karl von Frisch, *Bees: their vision, chemical senses, and language*, revised edition. Copyright © 1950, 1971, by Cornell University. Used by permission of the publisher, Cornell University Press



of color and scent, he then replaced it with a box bearing either the familiar scent or the familiar color and observed which box returning foragers tended to visit. In this experiment, the foragers chose the familiarly scented box over the familiarly colored box. Similar types of manipulative experiments, albeit with more factorial complexity, have been applied to understanding the prioritization of floral color vs. scent in honeybees (e.g. Gould 1993), bumblebees (Odell et al. 1999), and solitary bees (e.g. Burger et al. 2010). Likewise, an assessment of the relative roles of visual vs. olfactory stimuli have been richly explored in relation to perception of pollen rewards (e.g. Dobson and Bergström 2000; Lunau 2000).

While this “sensory dissection” approach can help estimate the strength of pollinator-mediated selection on floral color vs. scent (Klahre et al. 2011), or how particular stimuli change in relevance at different spatial scales (Streiner et al. 2009; Balkenius and Dacke 2010), it does not deliver a comprehensive answer to the question of how bees use floral scent and color. First, it is difficult to extract general principles about bees’ relative reliance on scent vs. color from their responses to a particular suite of colors and scents, because, as in the case of scent overshadowing color noted above, the answer will depend upon the relative salience of each stimulus chosen by the experimenter (Shettleworth 1998; Tang and Guo 2001; Giurfa 2007). Second, a complete dissociation of color and scent may mask important interactions only observable when both are present in concert (Hebets and Papaj 2005; Leonard et al. 2011a).

For example, a number of studies have shown that the mere presence of scent can facilitate color learning (Kunze and Gumbert 2001; Leonard et al. 2011b). Reciprocally, Gerber and Smith (1998) found that color modulates

olfactory learning in honeybees, even if it is not itself associated with reward (see also Balkenius and Kelber 2006; Hussaini and Menzel 2013). The ability of scent or color to modulate associative learning of the other modality may reflect non-elemental processes, because the enhancing stimulus is not itself unambiguously associated with the reward (Giurfa 2007). This form of non-elemental learning was elegantly demonstrated in a recent study by Mota et al. (2011). The authors used conditioning of the proboscis extension response (PER) to train harnessed honeybees to associate the presence of a particular scent with a sucrose reward. The bees were unable to associate color (e.g. blue or UV light) with sucrose; nonetheless, they were able to learn that the scent (1-nonanol) predicted reward in the presence of one color (blue) but not another (UV). Thus, even when color does not function as a conditioned stimulus, bees may still learn that it provides a context for responding appropriately to foraging-related olfactory stimuli.

When bees do form elemental associations between a reward, scent, and color, these cross-modal relationships are linked in memory. For example, Reinhard et al. (2004, 2006) have shown that scent can trigger recall of associated visual information. In one experiment (Reinhard et al. 2004), honeybee foragers gained experience with two feeders, each characterized by a particular combination of color and scent. In a test phase, the experimenters released one of these training scents inside the colony; in response, foragers visited the correctly colored feeder, even though it was itself now unscented. While the opposite phenomenon (a visual stimulus triggering recall of olfactory information) has not, to our knowledge, been demonstrated in bees, it has been shown in *Drosophila*. Guo and Guo (2005)

exposed flies to a combination of scent + visual pattern; after which flies were conditioned to avoid the pattern. Later, they also avoided the scent, which had not itself been associated with punishment.

Attention and perception

Multisensory stimuli are broadly thought to influence attention via both “bottom up” (stimulus-driven) and “top-down” (e.g. goal-related) processes. We focus largely on stimulus-driven effects, but direct those interested in top-down effects to the excellent review by Talsma et al. (2010). From a bottom-up perspective, we expect that a bimodal stimulus should be more salient to bees than a unimodal stimulus (Rowe 1999; van Swinderen and Greenspan 2003). Recently, using electroantennogram recordings, color-space metrics and behavioral assays, Katzenberger et al. (2013) established that the saliency of a color–scent compound to bumblebees is greater than that of each single stimulus and can usually be predicted in an additive fashion from its components. Notably, low-salience scents and colors in combination had higher salience than predicted by simple summation, a finding that resonates with research on super-additivity at the neuronal level in vertebrate systems (Stein and Meredith 1993; Alais et al. 2010). Likewise, research on floral constancy suggests that multisensory flowers (i.e. those that differ from neighbors in both color and scent) appear to compete for a bumblebee’s attention more effectively than unimodal flowers (Gegeer 2005).

What effect might these processes have on bees’ perception of flowers? Recent findings from other systems suggest that visual and olfactory perception may operate less independently than previously thought. Infamously, wine experts described the scent of white wines using red wine terminology when experimenters dyed the beverage red (Morrot et al. 2001). Subsequently, a growing body of research on human perception suggests that visual stimuli can indeed affect olfactory perception (de Araujo et al. 2005), or, “the nose smells what the eyes see”. Subjects detect an odor more quickly and identify it more accurately if paired with semantically congruent imagery (Gottfried and Dolan 2003); further, transcranial magnetic stimulation of the visual cortex improves olfactory discrimination (Jadaui et al. 2012). Although little is known about color’s effect on olfactory perception in invertebrates, calcium imaging of hawkmoths has shown that certain colors can either enhance or suppress MB activity in response to particular scents (Balkenius et al. 2009). In *Drosophila*, olfactory acuity is enhanced by certain aspects of the visual environment (e.g. flies are better able to localize an invisible odor source in the presence of vertical edges or textured background; Frye et al. 2003), giving rise to the argument

that vision and olfaction are not independent from each other in this species as well (Stewart et al. 2010).

Scents can also modulate visual perception, or “the eyes see what the nose smells” (Small 2004). In humans, there is evidence these effects may be reflexive, “bottom-up” processes. Using a binocular rivalry paradigm, Zhou et al. (2010) showed that when each eye is shown a separate image (a rose vs. a marker pen), exposure to the congruent scent (e.g. rose scent) promotes visual dominance of the congruent image (rose image over pen image). Interestingly, this effect occurs independently of the “top down” semantic linkage between visual and olfactory stimuli. When subjects were given purified water to sniff, but instructed that they were smelling a “rose” scent, the matching visual image (of a rose) did not obtain dominance. Bottom-up linkages between particular scents and visual images might thus reflexively guide visual perception, independently of conscious awareness. Likewise, humans show bottom-up olfactory enhancement of visual search tasks (Chen et al. 2013). In hawkmoths, olfactory stimulation enhances responsiveness to visual stimuli (Goyret et al. 2007), and in *Drosophila*, scents appear to affect attention to optic flow cues (Chow et al. 2011). As a whole, these findings suggest that by focusing on single modalities, we may be underestimating bee performance on search tasks, and missing opportunities to understand multisensory perceptual linkages.

Sensory ecology

How are the mechanisms of multisensory integration affected by real-world conditions? Both features of the environment (Dyer and Chittka 2004a; Streinzer et al. 2009; Dyer et al. 2011) and of the plant species itself (e.g. Spaethe et al. 2001) will affect the saliency, sequence, and degree of overlap between visual and olfactory stimuli relevant to bees. To add to this complexity, we anticipate both inter- and intraspecific variation in both olfactory and visual sensitivity (Spaethe and Chittka 2003; Balkenius et al. 2006; Spaethe et al. 2007; Burger et al. 2013). Flexibility in the timing and ordering of scent and color are thus a basic feature of bees’ foraging routines under natural conditions. Understanding to what degree this temporal variation matters for multisensory integration is an important but largely unaddressed question (Stein and Meredith 1993; Leonard and Hedrick 2010; Uy and Safran 2013). Research in this area would be useful for understanding what effect, if any, olfactory priming in the colony has upon later use of visual and olfactory information. More broadly, bees might be an ideal model system for understanding temporal dynamics of multisensory processing, given the ease which we can manipulate the timing of stimulus presentations and their easily accessible nervous systems.

A second approach towards understanding mechanisms of multisensory integration in natural settings is to introduce some degree of perceptual uncertainty to the tasks we ask bees to perform (Lynn et al. 2005). Rather than discriminating between single molecule scents, as is common experimental practice, bees are more likely to contend with scents that are complex blends, subcomponents of which may be shared across co-flowering plant species (Raguso 2008). Likewise, a foraging bee moving through sun and shade will have to perform color discrimination tasks under light levels that vary in both space and time. Does increasing the perceptual uncertainty associated with stimuli in one modality affect the use of stimuli in a second—or even third—modality? Given that the difficulty of the discrimination task determines whether bees use elemental or configural processing strategies in relation to unimodal compounds (Deisig et al. 2002), it may be worth exploring whether bees also show different strategies of multisensory integration when we give them tasks that approach the difficulty of discrimination under natural circumstances.

Development of multisensory integration

How multisensory perception develops is a major question for experimental biologists (Partan 2013), but to date research has been largely limited to vertebrates (Stein 2012). Older humans, for example, integrate auditory and visual stimuli over a longer temporal window (Laurienti and Hugenschmidt 2012). Yet there are good reasons to expect that invertebrates offer ample opportunities to tackle this question. In *Drosophila*, mechanisms of multisensory integration show changes over the course of development. While adults exhibit visual modulation of olfactory learning, and can form olfactory memories that depend upon visual stimuli (Guo and Guo 2005), Yarali et al. (2006) found that this was not the case for larvae, whose olfactory processing appears to be “insulated” against visual modulation. Might we find similar themes in the development of multisensory processing in bees, which also may proceed through phases marked by dramatically different sensory environments? After all, bee MBs show well-established patterns of change with both age and experience (Fahrbach 2006). In honeybees, MB growth corresponds to a shift to foraging outside the colony (Farris et al. 2001), and in bumblebees it may be similarly associated with the changing sensory environments experienced during early adult life (Riveros and Gronenberg 2010). In both groups, adult bees spend the first days or weeks of adult life in a dark environment dominated by olfactory stimuli. Upon foraging, bees enter a multimodal world. What changes might occur in how bees use vision and olfaction during these developmental transitions? Research on the relative

importance of visual and olfactory cues used by solitary oligolectic bees (e.g. Megachilidae) as they gain foraging experience with host plants suggests shifts can occur (Dötterl and Vereecken 2010; Milet-Pinheiro et al. 2012); however, most research described in the previous section uses experienced foragers as subjects. Given evidence that the way in which honeybees learn about unimodal compound stimuli changes with experience (Giurfa et al. 2003), what changes in multisensory integration might result from age and/or foraging experience?

Likewise, how developmental conditions might affect later use of color and scent remains an open question in bees. For example, after emergence *Bombus* workers spend variable amounts of time in their underground nest before experiencing a visually rich foraging environment. Recently, Jones et al. (2013) discovered that bumblebee workers housed in dark for the first week after emergence showed significantly larger volumes of MB calyces than bees exposed to visual stimuli during this time. What consequences might these volume differences have for multisensory integration?

The most direct investigation of possible developmental changes in multisensory integration comes not from bees, but from hawkmoths (e.g. *Manduca sexta* and *Macroglossum stellatarum*). Not only have researchers directly compared naïve vs. wild individuals' use of visual and olfactory cues (Raguso and Willis 2002, 2005), but using calcium imaging, Balkenius and Hansson (2012) have begun to chart training-related changes in the activation patterns of MBs that seem to be specific to multimodal stimuli. From a developmental perspective, Goyret et al. (2009) established that larval nutrition (beta carotene availability) can affect adult responsiveness to visual vs. olfactory stimuli. Given linkages between larval nutrition, body size, and visual vs. olfactory sensitivity in many bee species, there is no shortage of ontogenetic lines of inquiry waiting to be addressed.

Function: does use of multisensory stimuli increase bee fitness?

Regardless of how bees use both vision and olfaction when foraging, do they benefit from doing so? Most experiments assessing the adaptive significance of multimodal stimuli use free-flying behavioral assays where an array of artificial flowers is presented under standard environmental conditions to individual workers from captive colonies. A common fitness proxy is nectar collection rate (Burns and Dyer 2008) or one of its determinants—such as accuracy, decision speed, learning speed, or long-term memory. Although colony-level fitness is not usually measured, these simplified foraging scenarios assume that over the course of many foraging trips, even a small boost to nectar collection rate

could scale up to affect colony-level reproductive success (Pelletier and McNeil 2003).

Detection

A bimodal stimulus may be processed more quickly than a unimodal stimulus (Rowland et al. 2007; Balkenius et al. 2009; Leonard et al. 2012); as noted earlier, it may also be easier for bees to locate against a background of sensory or environmental “noise”. In humans, multimodal stimuli facilitate visual search (Van der Burg et al. 2008, 2009), and although both honeybees and bumblebees are amenable to similar experimental protocols (Spaethe et al. 2006; Morawetz and Spaethe 2012), to what degree multimodal stimuli affect their visual search strategies is unknown.

Apart from speed, the benefit of using both scent and color to locate flowers may be most apparent in the face of changing environmental conditions. For example, Kaczorowski et al. (2012) trained bumblebees to discriminate between two similarly colored rewarding and unrewarding flower types either in the presence or absence of accompanying floral scents. In a test phase where light levels were decreased, accuracy declined among bees when flowers were unscented, but not among bees whose flowers differed in both color and scent. Although analogous shifts between reliance on different sensory modalities have been demonstrated in vertebrates (rev. Smith and Evans 2013), this appears to be the first evidence that bees can adaptively shift reliance on color vs. scent depending on environmental conditions. Whether bees might shift towards using visual stimuli in environments where olfactory stimuli are “noisy” or degraded by airborne pollutants (McFrederick et al. 2009) is an obvious question.

Discrimination

Even in the absence of environmental changes, a number of recent experiments have shown that bees discriminate more accurately between rewarding vs. unrewarding flower types when they differ in both visual and olfactory characteristics. Using both scent and color might enhance foraging decisions by providing bees with additional sources of information (e.g. redundant indicators of floral identity), or by perhaps enhancing attention paid to a visual learning task (Kunze and Gumbert 2001; Leonard et al. 2011a). Using a Signal Detection Theory framework, Leonard et al. (2011b) showed that when trained in a color discrimination task, bees acted as though more certain about the color of the rewarding flower type in the presence of floral scent. The decrease in uncertainty would likely benefit nectar-foraging bees, who are able to maintain a high rate of “correct detections” of a more rewarding flower type while avoiding costly “false alarms” (landing on unrewarding, visually

similar, flowers such as Batesian mimics) (Lynn et al. 2005). There is even evidence that if flowers do not provide scents useful in visual discrimination tasks, bees may add their own repellant scent marks to unrewarding flower types (Giurfa et al. 1994).

Finally, while multimodal floral signals may separately affect search speed and decision accuracy, these two components of foraging performance are expected to trade off against each other (Chittka et al. 2003; Dyer and Chittka 2004b; Burns and Dyer 2008). Kulahci et al. (2008) compared foraging performance of bumblebees trained on artificial flowers that were different in reward value and were distinguished by shape differences, scent differences, or differences of both types. While the sensorial complexity of a floral display did not affect the shape of the speed-accuracy trade-off itself, bees made more accurate choices for a given decision time when flowers differed multimodally.

Evolution: multisensory integration and pollination mutualisms

When formulating questions regarding the mechanisms, development, and function of multisensory integration, it is worth remembering that each of these levels of analysis itself has an evolutionary history. More specifically, our understanding of how bees use color and scent is grounded in the fact that floral displays have coevolved with the sensory and perceptual systems of their pollinators. Although floral signal evolution is a thriving area of inquiry (e.g. Schaefer and Ruxton 2010; Leonard et al. 2012), a “receiver evolution” perspective has received less direct attention (with perhaps the notable exception of work on color vision; e.g. Chittka and Menzel 1992; Chittka and Briscoe 2001). Nonetheless, an evolutionary perspective on the relationship between bees and the floral stimuli can enhance the study of multisensory integration in several ways.

First, we can draw upon a rich body of knowledge to ask how multisensory integration of scents and colors in bees has evolved in relation to its neural substrate, the MBs (Strausfeld 2012). For example, comparative anatomical and functional approaches might be used to test hypotheses regarding the origin and subsequent fine-scale elaboration of MB sensory integration pathways (Strausfeld et al. 1998, 2009; Farris 2013). One could add a developmental perspective into this line of inquiry by comparing the development of multisensory integration in MBs across bee taxa that vary in relevant life history traits (e.g. social species that remain in a dark colony before foraging, vs. solitary species that quickly transition to foraging).

Second, we can consider multisensory integration in the context of a pollination mutualism, in which we expect

to see themes of both cooperation and conflict (Bronstein et al. 2006; Leonard et al. 2013). The colors and scents chosen by experimenters may be fairly arbitrary, but there is growing evidence that many aspects of multisensory floral displays may have evolved to exploit pre-existing perceptual biases (Schiestl et al. 2010; Schaefer and Ruxton 2010). We now appreciate that preferences for the colors, patterns, and scents commonly found in floral displays in many cases may have predated the origins of angiosperms (e.g. Biesmeijer et al. 2005; Schiestl 2010). Does the evolutionary history of these stimuli matter for understanding their integration? The answer to this question would shed light upon themes of constraint and flexibility in the evolution of perceptual systems. One could ask whether our understanding of the roles scent and color play changes, for example, if we use a scent like geraniol that is also a component of pheromones used by bees for intraspecific communication. Or, given that plant biosynthetic pathways link pigment and scent production (see Katzenberger et al. 2013), do patterns of multisensory integration change when we use particular combinations of scents and colors that bees might be more or less “prepared” for?

Future prospects

As presented from the perspectives of mechanism, development, function, and evolutionary history, multisensory integration in bees at this point involves more questions than answers. Fortunately, in each case, the tools and techniques needed to tackle these questions are within reach, and the answers are likely to be of major interest to researchers in other systems.

On a methodological note, changes to common learning protocols have recently been published that may kindle new interest in multisensory research. It is now possible to efficiently perform PER conditioning on honeybees and bumblebees with intact antennae, to both color and scent (Dobrin and Fahrbach 2012; Riveros and Gronenberg 2012). More than ever before, it should be straightforward to use carefully controlled presentations of color and scent to tackle questions relating to the temporal synchrony of color vs. scent (e.g. Mota et al. 2011). Other developments are perhaps similarly useful in designing free-flying behavioral assays, such as RFID readers and the use of real floral pigments as visual stimuli (Katzenberger et al. 2013). Further, since it is now possible to alter scent or pigment in living flowers by silencing the genes responsible for their production (Spitzer et al. 2007) we can test pollinator responses to flowers transmitting various suites of stimuli in increasingly realistic scenarios (Kessler et al. 2008, 2013; Klahre et al. 2011; Sheehan et al. 2012). These technical advances dovetail with growing interest in multimodal stimuli within and beyond our field.

As an example of how a multimodal approach might spur new thinking about classic questions, consider the relationship between the sensorial complexity of a flower and floral constancy. Constancy has captured the attention of scientists for centuries (rev. Chittka et al. 1999) and is of interest from the perspectives of both bee cognition and pollination ecology. However, most experiments to understand its drivers involve artificial flowers differing in a single aspect (e.g. color), or real flowers differing in multiple, uncharacterized, aspects. Gegear's (2005) finding that constancy increases when artificial flowers differ in multiple characteristics suggests an ecologically relevant assay for letting the bee “tell us” how different her perception of flowers varying in colors, scents, or both truly is. This approach could be used in experiments to quantify the perceived strength of particular components of a floral display, within and across modalities, with implications for understanding aspects of bee cognition and floral signal evolution.

We hope these factors will encourage more researchers to focus on understanding how and why bees use multisensory floral stimuli. Clearly, a century after von Frisch's pioneering studies of the visual and chemical senses of bees, there is no shortage of opportunities to continue his legacy by exploring the inner workings of their truly multisensory worlds.

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