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Influence of Ambient Illumination on the Use of Olfactory and Visual Signals by a Nocturnal Hawkmoth During Close-Range Foraging

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Synopsis As a goal-directed behavior, foraging for nectar functions on the basis of a sequence of innate stereotyped movements mainly regulated by sensory input. The operation of this inherited program is shaped by selective pressures acting on its efficiency, which is largely dependent upon the way the system handles sensory information. Flowers offer a wealth of signals, from odors acting as distant attractants, to colors eliciting approximation and feeding responses, to textures guiding feeding responses toward a reservoir of nectar. Thus, animals use different signals in the regulation of particular motor outputs. Nevertheless, the use of these sensory signals can be user-specific (e.g. species, motivation, experience, learning) as well as context-dependent (e.g. spatiotemporal patterns of stimulation, availability of signals, multimodal integration). The crepuscular/nocturnal hawkmoths *Manduca sexta* experience a wide range of illuminations during their foraging activity, which raises the question of how these environmental changes might affect the use of two important floral signals, odor and visual display. In a flight cage, we explored the use of these signals under different illuminances. Under conditions of starlight and crescent moonlight, moths showed very low levels of responsiveness to unscented feeders (artificial flowers). However, responsiveness was recovered *either* by increasing illumination, *or* by offering olfactory signals. Additionally, we recorded a bias toward white over blue feeders under dim conditions, which disappeared with increasing illumination. We discuss how this kind of experimental manipulation may provide insights to the study of how innate behavioral programs, and their underlying neural substrates, overcome selective forces imposed by the uncertainty of natural, ever-changing environments.

Introduction

In the past several years, there has been an increasing interest in the use of multiple sensory signals by animals (Senkowski et al. 2008; Hebets 2011). Multimodal sensory information allows animals engaged in goal-directed behaviors to respond to dynamic environments and may influence the perception and processing of specific information (Gegear 2005; Hebets and Papaj 2005). In experimental settings, animals are sometimes capable of using information from a single sensory modality in systems offering multimodal signaling; nevertheless, the ability to integrate multiple signals and consequently adjust behavior allows organisms to respond more

efficiently to highly uncertain natural conditions (Baerends 1950; Helsen et al. 2000; Raguso 2004; Hebets and Papaj 2005; Kulahci et al. 2008). Thus, multimodal sensory assessment is prevalent across animal taxa in goal-oriented tasks such as detecting competitors (Narins et al. 2005; de Luna et al. 2010), as well as searching for potential mates (Jennions and Petrie 1997; Taylor et al. 2007), food (Baerends 1950; Raguso and Willis 2002; Guerenstein and Lazzari 2009), or shelter (Warrant et al. 2004).

For pollinators, flowers offer a wealth of sensory signals, including volatiles, colors, sizes, shapes, textures, and even gradients of relative humidity and

carbon dioxide (Kevan and Lane 1985; Kelber 1997; Raguso 2004; Goyret and Raguso 2006; Chittka and Raine 2006; Goyret et al. 2008a; von Arx et al. 2012). However, the use of different stimuli can differ across scales and contexts (Balkenius et al. 2006; Goyret et al. 2008a), and may become superfluous, redundant, additive, or synergistic under different conditions (Raguso and Willis 2002; Partan and Marler 2005; Goyret 2008). Moreover, the ability to detect different types of stimuli might be particularly important for pollinators exposed to environments in which the availability of different signals can change drastically (e.g. wind, obstacles, illumination).

Manduca sexta (Sphingidae) are nectar-feeding, crepuscular/nocturnal hawkmoths that are native to the Americas and that pollinate crepuscule-blooming flowers that remain open overnight (Grant and Grant 1983). These moths use a wide range of sensory modalities to locate and handle flowers, including perception of CO₂ (Thom et al. 2004; Goyret et al. 2008a), humidity (von Arx et al. 2012), floral volatiles (Raguso and Willis 2002), visual display (Goyret et al. 2008b), and tactile stimulation (Goyret and Raguso 2006; Goyret 2010). However, searching for flowers by *M. sexta* is predominately driven by vision and olfaction (Brantjes 1978; Raguso and Willis 2002; Goyret et al. 2007), as in many other insects (Kevan and Baker 1983; Odell et al. 1999; Ômura and Honda 2005). *Manduca sexta* are capable of color vision, despite low availability of light, and show an innate preference for blue flowers (Cutler et al. 1995; Goyret et al. 2008b); they can also evaluate achromatic signals (i.e., brightness contrast), preferring more reflective flowers (Haber and Frankie 1989; Cutler et al. 1995). Experiments examining the role of visual and olfactory stimulation in the foraging behavior of *M. sexta* have suggested that they operate synergistically when co-occurring (Raguso and Willis 2002). Nevertheless, the manipulation of spatiotemporal patterns of olfactory and visual stimulation strongly influences foraging behavior in wind tunnels (Goyret et al. 2007). These results underscore the role of odor as a distant attractant, but also show the ability of olfactory signals to promote close range, visually guided responses.

Nocturnal foragers such as *M. sexta* face conditions of illumination that vary over orders of magnitude from sunset through the night, and across the lunar cycles, which strongly impact the visual properties of flowers (Johnsen et al. 2006). This could potentially influence the relative role of olfactory and visual signals from flowers during foraging. In this study, we evaluated the responses of *M. sexta* to either scented or unscented feeders

under four different illuminances that resembled natural, ecologically relevant settings ranging from starlight to gibbous moonlight. Additionally, by offering a white and a dark-blue feeder against a dark-green background, we explored the role of chromatic and achromatic signals in the innate preferences of *M. sexta* as a function of illuminance. Finally, in a second experiment we evaluated the effect of illuminance and presence of olfactory signals on the timing of the onset of activity (warm-up and flight) of moths at the beginning of their scotophase.

Methods

Animals

We obtained a constant supply of *M. sexta* eggs from our breeding chamber at Cornell University, Ithaca, NY. Caterpillars were reared at a photoperiod of 16L:8D and on an artificial diet (Bell and Joachim 1976), modified as described by Goyret et al. (2009) to avoid β -carotene deficiency. Male moths were housed in one screen cage and females in another and were kept in different Precision Model 818 Refrigerated Incubators (Thermo Fischer Scientific Inc., Waltham, MA). Each cage was 45 × 45 × 45 cm (BioQuip Products, Inc., Rancho Dominguez, CA). All experiments involved flower-naïve *M. sexta* starved for 2–4 days after eclosion.

Experimental arena

We conducted experiments in a flight cage 95 × 95 × 95 cm. The back and sides of the cage consisted of black and dark-green fabric (fern patterned) and its front consisted of a clear plastic sheet to allow for observations. The cage was illuminated from the ceiling using a homogeneous mixture of cold (7500 K) and warm (3000 K) white LEDs (Ledtronics, Torrance, CA). We controlled brightness of the LEDs with a GPS-30300 linear DC power supply (GW Instek America Corp., Chino, CA); light entered the cage after being scattered by a plastic diffuser that covered the entire ceiling.

Experimental treatments

Odor treatments: At the base of the stand of the feeders (height: 15 cm), we placed a cotton swab that was either scented (odor treatment) with two drops of bergamot oil (NOW Foods, Bloomingdale, IL) or unscented (no odor treatment).

Light treatments: We set four illuminance levels as measured at the height of the feeders by setting an SED100 detector with W13895 input optics and Y30367 photopic filter to measure photopic illuminance with a ILT1700 radiometer/photometer (all

instruments from International Light Technologies, Peabody, MA). Each light treatment was named after an approximate natural condition using Johnsen et al. (2006) as reference: “starlight” (0.0018 lux), “crescent moon” (0.0105 lux), “quarter moon” (0.0671 lux), and “gibbous moon” (0.2350 lux). Illumination levels are hereafter referred to by their qualitative description rather than by their illuminance.

Procedure used for the feeding experiment

We conducted feeding experiments from March to July 2012 and from October 2012 to May 2013. We placed two feeders (see Pfaff and Kelber 2003) in the center of the flight cage so that the “flowers” were approximately 25 cm above the ground. Both feeders offered the same 1% (w/w) sucrose solution, but one was blue and the other one was white to the human eye (reflectance spectra described by Goyret et al. 2008b). Moths were placed in individual transfer cages 1 h before the start of the experiment. Each moth was pseudorandomly assigned to a combination of one odor treatment and one light treatment, released individually in the flight cage, and allowed 300 s to become active (each moth was tested only once). If a moth did not become active during that period, it was discarded from the experiment. If a moth took off within that period, we allowed it to fly for 180 s. If during those 180 s, a moth did not probe on any feeder, we recorded it as unresponsive. We recorded the variable “responsiveness” as the percentage of moths that probed (for at least five consecutive seconds) out of the total flown. We also noted the latency as the time, to the nearest second, between flight and first feeding, as well as the color of the first feeder probed. After each trial, we swapped the positions of the feeders pseudorandomly.

Procedure used for the activity experiment

We performed the activity experiment from May to September 2012 at Cornell University with the same flight cage described for the feeding experiments. Moths were placed on the floor of the flight cage, where illuminance was somewhat lower than at the height of the feeders for the same settings of light as for the feeding experiment. At floor level, we measured 0.0001 lux (corresponding to “dim starlight” conditions), 0.0013 lux (starlight), 0.0073 lux (dim crescent moon), and 0.1241 lux (dim gibbous moon) (following Johnsen et al. 2006). LED lights were off under “dim starlight” conditions; otherwise LEDs were set to the corresponding “starlight”, “crescent moon”, and “gibbous moon” conditions as

measured at feeder height. A corresponding “quarter moon” illumination was not used. In trials with odor, we placed three drops of bergamot oil on a cotton swab at the center of the cage.

Animals were housed in separate transfer cages 1 h prior to the experiment. We placed these cages with an open top in the flight cage to allow the moths to fly. We conducted trials for the first hour of their scotophase. During this period, we recorded the latency (to the nearest minute) until warm-up (wing beating or walking) and first flight. A percent response was measured for activity and flight by dividing the number of moths that displayed the respective behavior by the total moths used in each treatment.

Statistical analysis

We analyzed the variable responsiveness for both the feeding and activity experiments using *G*-tests. We analyzed latency with a two-way ANOVA. To evaluate choice of flower color, we used binomial tests with the null hypothesis that each feeder is equally likely to be probed first (random choice). Because our data were not normally distributed in the activity experiment, the effects of odor and illumination on the latency until warm-up and until onset of flight were analyzed using the non-parametric Kruskal–Wallis test. Statistical tests were conducted using JMP (SAS Institute, Cary, NC) and SPSS (IBM, Armonk, NY).

Results

Feeding experiment

We flew a total of 243 animals consisting of 111 males and 132 females. In the absence of olfactory stimuli, there were strong differences in responsiveness across intensities of illumination ($G_h = 7.45$, $P = 0.0064$). Under the two higher levels of light (“quarter moon” and “gibbous moon”), responsiveness was similarly high ($G_h = 0.15$, $P = 0.69$). On the other hand, under the two lower levels of light (“starlight” and “crescent moon”), responsiveness was equally low ($G = 0.03$, $P = 0.8585$), but significantly lower than under the higher illuminations ($G = 7.26$, $P = 0.0071$; Fig. 1). When an odor cue was present, there were no differences in feeding responses across light intensities ($G_h = 0.51$, $P = 0.4736$). The presence of odor significantly increased feeding responses to the visual targets under “starlight” ($G = 5.87$, $P = 0.0154$) and “crescent moon” illuminations ($G = 4.21$, $P = 0.0403$), but had no apparent effect under brighter

illuminations (“quarter moon”: $G=0.45$, $P=0.5017$; “gibbous moon”: $G=0.50$, $P=0.4786$) (Fig. 1).

Latencies were not affected by the presence of odor ($F_{(1,127)}=0.007$; $P=0.936$), light conditions ($F_{(3,127)}=0.643$; $P=0.589$), or their interaction ($F_{(3,127)}=1.167$; $P=0.325$) (Table 1).

When comparing choices for color, moths showed a significant bias toward the white feeders under conditions of “starlight” (Binomial test; $P=0.0055$; $N=30$) and “crescent moon” ($P=0.0489$; $N=28$). Under conditions either of “quarter moon” or “gibbous moon”, choices did not differ from random probabilities ($P=0.12$; $N=38$ and $P=0.94$; $N=37$, respectively) (Fig. 2).

Activity experiment

For the activity experiment, we flew a total of 233 moths consisting of 117 males and 116 females. We found no effect of odor on the proportion of moths that warmed-up (G -test; $G=3.60$, $P=0.0577$, $N=233$) or flew ($G=2.0945$, $P=0.1478$, $N=233$). However, when comparing light treatments there was a significant difference both in the proportion of moths that showed warm-up behavior (scented: $G=22.66$, $P<0.0001$, $N=110$; unscented:

$G=21.13$, $P<0.0001$, $N=123$) and that flew (scented: $G=30.24$, $P<0.0001$, $N=110$; unscented: $G=38.18$, $P<0.0001$, $N=123$; Fig. 3). There were no differences between warm-up activity ($G=0.24$, $P=0.6233$, $N=120$) or onset of flight ($G=0.89$, $P=0.3463$, $N=120$) between the two highest light intensities: “dim crescent moon” and “dim gibbous moon”. Under “dim starlight” illumination, a smaller proportion of moths showed warm-up activity than under conditions of “starlight” ($G=10.61$, $P=0.0011$, $N=113$) or “dim crescent moon” ($G=28.14$, $P<0.0001$, $N=115$). These differences were paralleled by significantly smaller proportions of moths flying than under “starlight” ($G=21.75$, $P<0.0001$, $N=113$) or “dim crescent moon” ($G=43.42$, $P<0.0001$, $N=115$). At “starlight” illumination, moths were less active than at “dim crescent moon” illumination (warm-up: $G=4.87$, $P=0.0273$, $N=126$; flight: $G=4.52$, $P=0.0334$, $N=126$) (Fig. 3).

We found no effect of light on the latency of warm-up ($\chi^2=1.47$, $df=3$, $P=0.6887$) or latency of flight ($\chi^2=2.05$, $df=3$, $P=0.56$) and no effect of odor on latency of flight ($\chi^2=1.12$, $df=1$, $P=0.29$). Nevertheless, the presence of odor

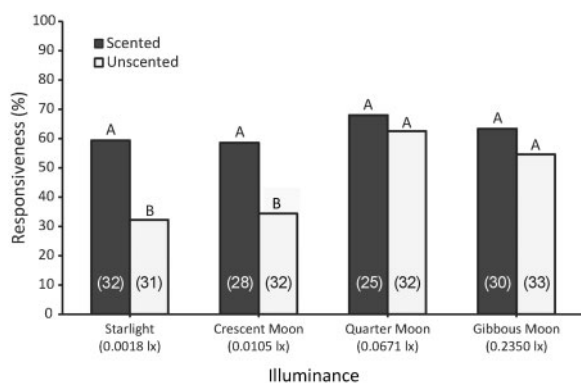


Fig. 1 Percent of moths that probed feeders (artificial flowers), for scented and unscented trials, under each tested condition of light. Different letters denote significant differences in responsiveness. Sample sizes are denoted by numbers within parentheses.

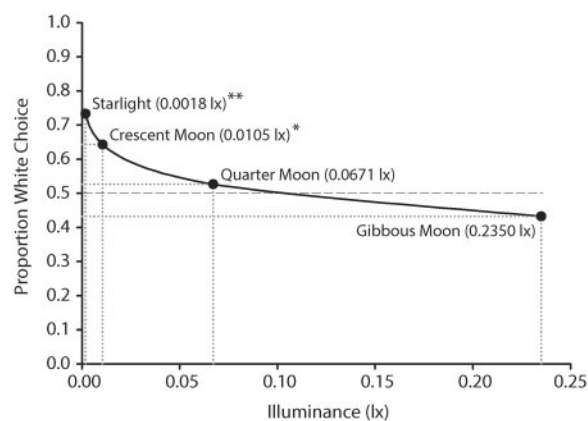


Fig. 2 Proportion of moths that probed the white artificial feeder first for each condition of light. Asterisks represent significant ($*<0.05$; $**<0.01$) departures from probabilities based on random choice.

Table 1 Number of responsive moths/total moths (N) and the median, mean, and standard error of the mean (SEM) for latency (seconds) in the feeding experiment

	Scented				Unscented			
	Starlight	Crescent	Quarter	Gibbous	Starlight	Crescent	Quarter	Gibbous
N	20/32	17/28	17/25	17/30	10/31	11/32	19/32	18/33
Median	54.0	42.0	31.0	31.0	45.5	60.0	33.0	36.5
Mean	60.9	66.2	48.2	42.1	45.4	72.6	45.2	61.6
SEM	7.92	12.94	11.12	8.40	8.16	18.49	8.98	12.88

appeared to slightly reduce the latency of onset of warm-up ($\chi^2=4.00$, $df=1$, $P=0.046$) (Table 2).

Discussion

Vision and olfaction under varying illuminances

Across all conditions of illumination in the presence of odor naïve moths responded well to our feeders with levels of responsiveness that were comparable to several previous experiments involving visual and olfactory signals in flight cages (Goyret and Raguso 2006; Goyret et al. 2008b, 2009; Goyret 2010). Feeding responses of *M. sexta* involve hovering, uncoiling of the proboscis, and its precise placement on

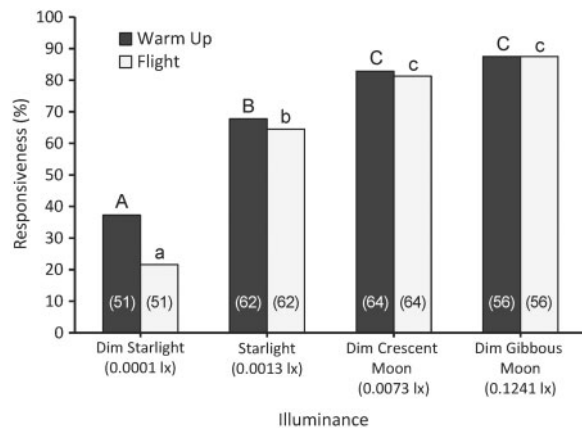


Fig. 3 Percent of moths that displayed warm-up or flight activity under each tested condition of light. Odor treatments were combined due to lack of significant effect ($P>0.05$). Upper-case letters denote significantly different values of responsiveness for warm-up and lower-case letters for flight. Sample sizes are denoted by numbers within parentheses.

the visual target. Thus, our results show that our feeders could be visually detected and were specifically probed as potential sources of nectar, even under extremely dim illuminations (Fig. 1). In unscented trials moths responded well to feeders when illumination was relatively bright, however, they responded poorly to those feeders under dim illumination (Fig. 1). This suggests that with dimmed illumination feeders lost their predictive value as indicators of potential sources of nectar. Our results indicate that, at close range, odor is not required in the evaluation of potential sources of nectar (brighter conditions), although it may compensate for equivocal visual detection, thus aiding in the response to flowers under very dim illuminations. These results are strikingly similar to those found in moths with reduced visual capacity resulting from a deficiency of vitamin A, where olfactory stimulation effectively compensated for partial visual impairment (see Goyret et al. 2009).

Natural environments under dim illumination present a wealth of equivocal visual targets, most of which have very small probabilities of being nectar sources. The costs of allocation of time and energy in the exploration of potential nectar sources could have selected for systems that mostly respond to conspicuous visual targets. On the other hand, the presence of floral odors is associated with higher probabilities of a nectar source, which could have selected systems that do respond to equivocal visual targets under these conditions. What could be the underlying mechanisms for such behavioral flexibility?

Table 2 Number of responsive moths/total moths (N) and the median, mean, and standard error of the mean (SEM) for latency (minutes) until warm-up and flight in the activity experiment

	Scented				Unscented			
	Dim Starlight	Starlight	Dim Crescent	Dim Gibbous	Dim Starlight	Starlight	Dim Crescent	Dim Gibbous
Warm-Up								
N	10/24	22/28	26/31	26/27	9/27	20/34	28/33	23/29
Median	6.5	8.0	9.5	12.5	12.0	14.0	15.0	17.0
Mean	8	12.2	15.2	11.9	17.4	18.5	16.8	17.2
SEM	2.53	2.60	2.97	2.34	4.00	4.14	3.18	3.59
Sig	A	A	A	A	B	B	B	B
Flight								
N	7/24	20/28	24/31	26/27	4/27	20/34	28/33	23/29
Median	16	18	23	15.5	26.5	18.0	18.0	20
Mean	19.7	18.7	21.4	14.9	28.5	23.3	19.8	20.7
SEM	7.45	4.18	4.37	2.93	13.25	5.21	3.75	4.31
Sig	a	a	a	a	a	a	a	a

Notes: Statistical significance (Sig) is denoted by different letters using upper case for values of responsiveness for warm-up and lower case letters for flight.

Mechanistically, these selective pressures might have favored the establishment of a visual-response threshold at a relatively high signal-to-noise ratio (above the absolute visual threshold) below which feeding responses based purely on vision remain inhibited. This is consistent with the stepwise increase in responsiveness observed in this study (Fig. 1, dark bars). It would be worthwhile to investigate whether the increase in responsiveness under olfactory stimulation is due to the override, or lowering, of this putative visual-response threshold via cross-modal neural integration. Findings of emergent patterns of neural activity in the mushroom bodies of *M. sexta* under concomitant exposure to visual and olfactory stimulation (Balkenius et al. 2009) appear to lend support to this hypothesis. Nevertheless, this neurophysiological finding may also suggest that the presence of odor might establish a novel, cross-modal percept through neural integration (Narins et al. 2005). These two hypotheses might not be mutually exclusive, as emergent cross-modal percepts could be the observed outcome of cross-modal disinhibition of unimodal thresholds of response.

Wild *M. sexta* in the Sonoran Desert under crepuscular lighting have been shown to respond maximally under both olfactory and visual stimulation (Raguso and Willis 2005). However, those wild individuals most likely had previous foraging experience. Learning and memory, as well as generalization might account for the apparent contradiction with our results with those from naïve moths. We are actively investigating whether previous experience on scented flowers could affect the results presented here.

Finally, it is worth stressing that our study focuses on close-range foraging, and it is important to note that olfactory signals can be essential during long-range search, when odor plumes can guide pollinators toward a source of nectar, thus enhancing the probability of encountering flowers (Goyret et al. 2007). In congruence with a vast body of work, we have previously shown in wind tunnels that *M. sexta* readily follow an odor plume emanating from a scented feeder, extending their proboscis toward it with high fidelity, while they respond extremely poorly to unscented feeders. Nevertheless, transient olfactory stimulation before takeoff significantly increases the probability of probing responses on an unscented feeder, showing that even brief olfactory stimulation can trigger a visually guided response to unscented feeders (Goyret et al. 2007). These findings could also be explained by the afore-stated hypothesis that olfactory stimulation could lower visual thresholds cross-modally. Moreover, they could justify the investigation of its temporal dynamics.

Manduca sexta continues to be an excellent model for exploring the poorly understood cross-modal integration of different sensory pathways at both physiological and behavioral levels.

Choice of flowers under varying illuminances

Manduca sexta are capable of visually detecting objects using both color (chromatic) and brightness (achromatic) signals (Cutler et al. 1995). In a recent study (Goyret et al. 2008b), we found evidence to suggest that the innate bias toward blue color during foraging by *M. sexta* is due to “true color vision” (evaluation of wavelength independently of brightness) rather than, as previously suggested, by stimulation of blue receptors (Cutler et al. 1995). Nevertheless, in that experiment, which involved naïve *M. sexta* and the same feeders utilized in the present study, we could not eliminate the possibility that the innate preferences for blue were based on detection of achromatic contrast. This is because our flight cages were white, thus offering a greater achromatic contrast to the darker blue feeder than to the white feeder. Interestingly, in the present study we found that at the two lowest illuminances tested, *M. sexta* showed a strong innate bias toward white flowers (Fig. 2). The dark green/black background in this experiment suggests that under very dim illuminances *M. sexta* preferred the higher achromatic contrast offered by the white feeder. As we increased illuminance, the bias disappeared, and moths’ innate preferences did not differ from random probabilities (Fig. 2). This might suggest that *M. sexta* do not have the ability to use chromatic vision under very dim conditions, differing from their close, strictly nocturnal relative, the hawkmoth *Deilephila elpenor*, which has been shown to use color vision under comparable conditions (Kelber et al. 2002). Alternatively, *M. sexta* may continue to see color at all illuminations, although in dim light they might rely on the strong achromatic contrast between the white feeder and the dark background as a more robust cue than provided by any chromatic difference. Under dimmer illuminations, the achromatic contrast between the white feeder and the dark background was maximal, which could explain the bias toward these feeders. The lack of a consistent bias with increased illuminance (which favors color perception) could reflect a conflict between innate preferences for blue chromatic signals and achromatic detectability of white feeders against a dark background.

In most species, limitations in photon catch and the corresponding challenges of photon-shot noise and dark noise, make achromatic vision more

effective than color vision in dim light (Vorobyev 1997). However, color signals can be reliable even at night (Johnsen et al. 2006; Kelber and Roth 2006). The ability to use both achromatic and chromatic vision has been demonstrated in the diurnal hawkmoth *Macroglossum stellatarum* for learned, rather than innate, preferences (Kelber 1996, 2005) and while using floral patterns during inspection of flowers (Goyret and Kelber 2011, 2012). We are testing moths' preferences to blue and white feeders against different backgrounds and different illuminances to better understand the role of chromatic and achromatic signals in the innate preferences of *M. sexta*. Additionally, learning experiments will allow us to evaluate which visual aspect of a nectar source, chromatic or achromatic contrast, are more salient under different backgrounds and illuminations, and whether a learned conditioned stimulus can be translated to different contexts (backgrounds and illuminances).

Onset of activity under varying illuminances and olfactory stimulations

Our results from the activity experiment show that decreasing illumination lowered the likelihood of activity (Fig. 3), whereas the presence of odor had a slight effect in reducing the latency of onset of activity (Table 2). It is possible that the potential gains in energy from foraging would be outweighed by the costs of the foraging activity under particularly dim conditions. Under “dim starlight” illuminations, moths were initially unable to efficiently navigate, and collided with walls and transfer cages for some seconds before displaying normal flying behavior. Limitations on the sensitivity of the eye to available light limits foraging in crepuscular (*Megalopta genalis*) and nocturnal (*Lasioglossum* sp.) bees (Kelber et al. 2006). *Manduca sexta* may similarly decrease active behavior if the availability of light is insufficient for efficient navigation. On the other hand, detection of odor appeared to stimulate appetitive behavior to some degree, which was suggested by the slightly shorter latencies of warm-up behaviors that typically precede flight. Finally, it is worth mentioning that our feeding experiments were conducted under illuminances that did not affect flight behavior in our activity experiment (Figs. 1 and 3).

Conclusions

Lacking an explicit representation of what constitutes a source of nectar, flower-naïve moths rely on sensory input to control stereotyped innate movements that increase their chances of encountering

nectar. This sensory control appears to be context-dependent, when spatiotemporal patterns of stimulation, availability of signal, and cross-modal (or multimodal) integration of sensory input allow the animal to cope with highly uncertain environments. Our results show that flower-naïve moths fail to evaluate detectable unscented visual targets as potential sources of food under very dim light. The fact that moths showed increased responsiveness to these feeders when they were either scented or under brighter illuminations, and that they appeared to use achromatic detection or innate color preferences, depending on light availability, underscores the innate behavioral flexibility of these animals. These behavioral phenomena offer insights toward understanding the selective pressures affecting the evolution of innate behavioral programs, the exploration of the neural bases underlying sensory integration, and ultimately, the effective distinction animals make of the subtle differences between the perception of stimuli and the gain of information.

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