Olfactory modulation of pre-flight shivering behavior in male moths

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1. Abstract

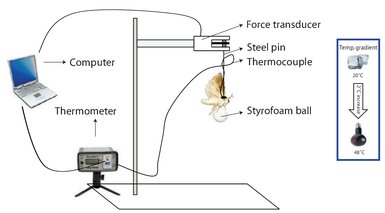
In nocturnal moths olfaction is the predominant sensory modality shaping many of the adult animal's activities, including reproduction. A two-component pheromone blend is sufficient to elicit the typical zigzag upwind flight behavior in *Helicoverpa zea* males. However, before flight can be initiated, the endothermic flight muscles must first be warmed-up by shivering. We investigated the influence of olfactory sensory input on this thermoregulatory behavior. An infrared camera placed above a small wind tunnel was used to record and measure the thoracic temperature changes in free animals that were exposed to odor blends varying in their composition (ranging from an attractive pheromone blend to an unattractive blend containing behaviorally antagonistic odorants). In addition, maximum vertical force per unit muscle mass as a function of thoracic temperature was determined in tethered flight with a force transducer. Male *H. zea* exposed to the attractive pheromone blend spent less time on the ground when shivering, warmed up at faster rates and took off at lower mean thoracic temperatures than those males exposed to other pheromone blend combinations. Force measurements demonstrated that these lower thoracic temperatures exhibited by males exposed to the attractive pheromone blend, correspond to low maximum vertical force production when compared to the other treatments. Since there is an optimal thoracic temperature for flight, these results indicate that male moths are prepared to compromise optimal flight efficiency with the possibility of being the first to arrive at a receptive female.

2. Introduction

Attractive, unattractive and even repulsive scents are environmental cues that allow animals to assess the presence of a particular resource (e.g., food or mates) and how they will react to it. Strong selective pressures act on this olfactory behavior which includes the decision of whether or not to approach the olfactory stimulus and an efficient and successful location of the source. How olfactory stimuli influence motor behavior is an important question of sensory motor integration. In this study, we investigated the warm-up behavior of the moth *Helicoverpa zea* when sensing different odors based on pheromone blends.

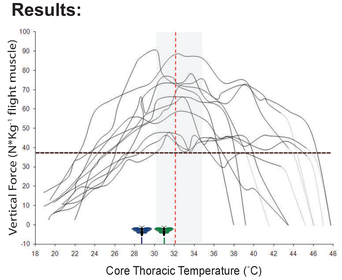
3. Power Production of Flight Muscles at Different Temperatures

Experimental Setup: Force Transducer



- Vertical force production was measured with a force transducer.
- Thoracic temperature was monitored by a thermocouple.
- Force and temperature were simultaneously recorded on a computer.

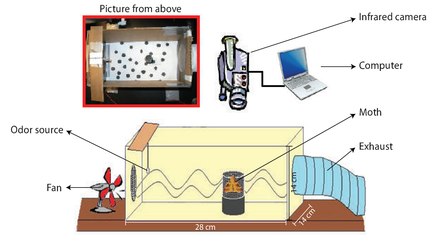
Results:



- Maximal vertical force production as a function of core thoracic temperature (N=11).
- Horizontal brown line = mean vertical force needed to counteract the mean body mass.
- Vertical red line = mean temperature at which the mean maximal vertical force is exerted.
- Blue moth = Attractive blend (see Panel 4).
- Green moth = Non-Attractive and neutral blends (see Panel 4).
- Shaded area = Range of maximal force production for all individuals tested.

4. Warm-up Behavior Elicited by Different Olfactory Stimuli

Experimental Setup: Wind Tunnel

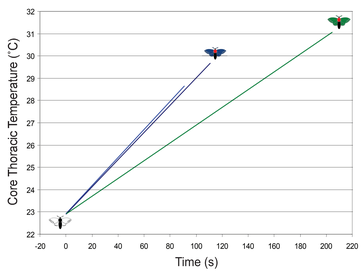


- Thoracic temperature in untethered animals was measured with an infrared camera.
- Olfactory stimuli varied according to the different treatments (see below).
- Thoracic temperature at take-off, shivering time and heating rate were calculated.

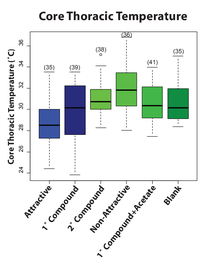
Treatments:

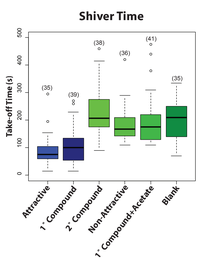
TREATMENT	CHEMICAL COMPOUND			
	(z)-11-hexadecenal	*(z)-9-hexadecenal*	*(z)-11-hexadecenyl acetate*	*Hexane*
Attractive blend	✓	✓		
1º Compound	✓			
2º Compound		✓		
Non-Attractive blend	✓	✓	✓	
1º Compound+Acetate	✓		✓	
Blank				✓

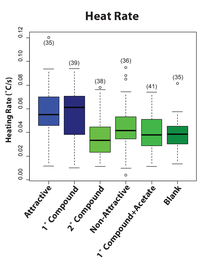
Results:



- Core thoracic temperature as a function of time (N≥35 per treatment).
- Light blue = Attractive blend (treatment1).
- Dark blue = 1˚ Compound blend (treatment 2)
- Green = Mean of treatments 3-6.







5. Conclusions

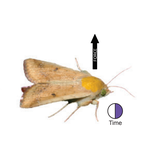
a. Male moths exposed to the attractive pheromone blend take off at a lower thoracic temperature, shiver for a shorter period of time, and warm up at a faster rate than those exposed to other blend combinations.

b. Males which take off with a thoracic temperature of 28.6ºC, such as the males that responded to the attractive blend, generate less maximal vertical force than those with a thoracic temperature of around 31.1ºC, as observed in males that were not exposed to the attractive stimulus.

6. Discussion

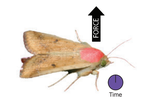
GOOD
(Attractive blend)
or
SUBOPTIMAL
(1º compound)

HIGH heating rate



BAD
(Non-Attractive blend)
or
NEUTRAL
(Treatments 3,5&6)

LOW heating rate



- Taken together, these data suggest that sexual pheromone cues modulate shivering behavior, muscle temperature at take-off and consequently flight performance during tracking of the olfactory signal.
- The safety factor for flight is substantially reduced in moths stimulated with the attractive scent, which must generate a trade-off between rapid departure at a suboptimal temperature and delayed take-off with greater performance.

7. Future Research

Characterize the flight-associated neuromuscular activation pattern in male moths exposed to attractive, suboptimal and non-attractive olfactory cues in similar environmental conditions as those of the behavioral assays.

8. Acknowledgements

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