Journal of Insect Physiology 96 (2017) 115–121

Contents lists available at ScienceDirect

Journal of Insect Physiology

journal homepage: www.elsevier.com/locate/jinsphys

Flight motor modulation with speed in the hawkmoth *Manduca sexta*

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ARTICLE INFO

Article history:
Received 8 July 2016
Received in revised form 12 October 2016
Accepted 13 October 2016
Available online 29 October 2016

Keyword:
Manduca sexta, electromyography
flight
speed
power
biomechanics

ABSTRACT

The theoretical underpinnings for flight, including animal flight with flapping wings, predict a curvilinear U-shaped or J-shaped relationship between flight speed and the power required to maintain that speed. Experimental data have confirmed this relationship for a variety of bird and bat species but not insects, possibly due to differences in aerodynamics and physiology or experimental difficulties. Here we quantify modulation of the main flight motor muscles (the dorsolongitudinal and dorsoventral) via electromyography in hawkmoths (*Manduca sexta*) flying freely over a range of speeds in a wind tunnel and show that these insects exhibit a U-shaped speed-power relationship, with a minimum power speed of 2 $m\,s^{-1}$, indicating that at least large flying insects achieve sufficiently high flight speeds that drag and power become limiting factors.

1. Introduction

Well-established aerodynamic theory predicts a curvilinear relationship between flight speed and the power required for flight in animals and machines, (e.g. Ellington, 1991; Pennycuick, 1968). This U-shaped relationship specifies two quantities of particular physiological and ecological importance, the minimum power speed, i.e. the speed which minimizes cost per unit time and is the optimal speed for flight activities which require loitering in one location and the maximum range speed, which minimizes cost per unit distance and is the optimal speed for activities such as foraging or migration (Fig. 1). Experimental support for this theoretical relationship has been found in birds (Tobalske et al., 2003; Ellerby and Askew, 2007; Morris and Askew, 2010) and bats (von Busse et al., 2013). However, evidence in insects is absent or contradictory, possibly due to differences in physical scale and physiology between birds, bats and insects. For example, limits to variation in flapping frequency or amplitude might prevent insects from flying fast enough to become drag-limited, or changes in body and wing orientation with speed might distort the expected U-shaped curve to a linear relationship. (See Fig. 2).

Insect flight is experimentally less tractable than vertebrate flight because only a few species have been trained to fly over a range of speeds in wind tunnels (e.g. Willmott and Ellington, 1997; Dudley and Ellington, 1990), small body size makes metabolic measurements based on oxygen consumption or carbon dioxide production in a wind tunnel challenging, techniques used in birds for direct muscle mechanical power output measurements rely on an endoskeleton, and the high flapping frequency of insects increases the difficulty of aerodynamic measurements such as particle image velocimetry in free-flying animals (e.g. Johansson et al., 2013). Given these obstacles it is perhaps not surprising that one of the few attempts to characterize the speed-power relationship in insects found essentially no relationship (Ellington et al., 1990), although a later re-analysis of those data combined with others selected from a variety of other sources, including tethered flight did support a U-shaped relationship (Nachtigall et al., 1995) in bees. Additionally, kinematic analysis of *Manduca sexta* flying in a wind tunnel support a U-shaped curve, but much of the underlying analysis framework relies on the same theories that produce a U-shaped curve in general so the finding is not particularly surprising nor can it demonstrate that other physiological trends do not compensate for the aerodynamic power to speed relationship (Willmott and Ellington, 1997).

Following these results, we hypothesize that flying insects do exhibit a U-shaped, curvilinear power-speed relationship and we test this by measuring the modulation of the flight motor muscles in the hawkmoth *Manduca sexta* during free flight across a range of speeds in a wind tunnel. In *Manduca*, modulation of the relative timing of activation of the opposing dorsolongitudinal (DLM) and dorsoventral (DVM) muscles is known to affect power input both *in vitro* and *in vivo* (Tu and Daniel, 2004; Springthorpe et al., 2012; Sponberg et al., 2012), and we hypothesize that these timing changes will be evident in our results. We found that changes in activation phase follow the expected U-shaped pattern, indicating

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http://dx.doi.org/10.1016/j.jinsphys.2016.10.003
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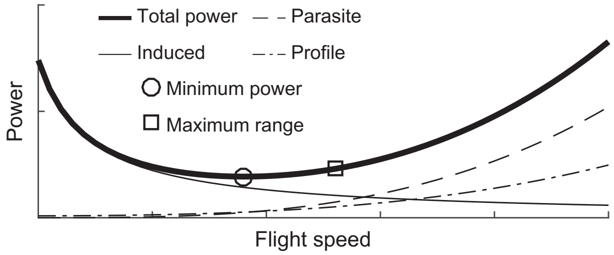

Fig. 1. Theoretical power requirements for flight, divided into the induced power (i.e. cost of generating lift), parasite power (overcoming body drag) and profile power (overcoming wing drag). The minimum power (i.e. lowest cost per unit time) and maximum range (lowest cost per unit distance) values are shown. Axes do not show quantities since the exact coefficients required are largely unknown. Furthermore, other aerodynamic models such as those based on unsteady flapping aerodynamics, may divide the induced and profile power components differently although the overall total power versus speed relationship remains similar.

that the fundamental flight speed to power relationship is present in hawkmoths and results in substantial variation in flight motor output over the range of speeds achieved by the animals during steady, untethered flight in a wind tunnel with a minimum power speed near 2 m s^{-1}.

2. Methods and materials

2.1. Animals

We obtained male *Manduca sexta* (Linnaeus 1763) pupae from the domestic colony maintained in the University of North Carolina at Chapel Hill Department of Biology and housed them in fabric mesh cages (30 × 30 × 30 cm) placed in an environmental chamber maintained at 25 ± 3 °C until eclosure. Males were selected from the colony due to slightly lower wing loading (i.e. mass to wing loading) leading to better flight performance as compared to females and to avoid mating activity in the holding chamber. Following eclosure, we maintained the adults in the same mesh cages under a 20:4 h light:dark photoperiod to minimize activity and avoid wing damage during confined flight.

Beginning 4 days after eclosure we began moth training, feeding them daily with an artificial nectar solution (1:4 honey:water) presented in an artificial flower constructed from a small white plastic funnel 2–4 cm in diameter attached to a 1 ml syringe body. The funnel was smooth-sided but had light yellow lines running from the center to the periphery. To train the moths to produce free and stable hovering, forward flight and feeding behavior in the wind tunnel, we placed quiescent moths on the feeder in the tunnel working section, added a natural flower stimulus (fresh white narcissus collected from campus gardens) to the working section, dimmed the room lights and waited for the moth to begin shivering its wings and extending its proboscis. Moths that did not exhibit this behavior within approximately 10 min were returned to the holding chamber and training was attempted again on the following day. Moths that completed warm-up shivering typically began to fly erratically in the tunnel and then approached the natural flowers with their proboscis extended. If the moth did not approach the flowers, they were moved toward the moth. Moths that exhibited no feeding interest within 5 min were removed to the holding chamber and training was attempted again the following day. Once the moth began trying to feed from the natural flower, we slowly moved it to lead the moth to the artificial flower and then quickly removed the natural flower. Many moths then began feeding from the artificial flower at this time. Those that did not were lured again with the natural flower until they succeeded in feeding from the artificial flower or tired, at which point they were returned to the holding chamber. Moths that did feed were allowed to do so for 15–30 s and then also returned to the holding chamber and fed again on two following days from the artificial flower only, or with a natural flower stimulus in the chamber if necessary to produce warm up. Most moths readily returned to the artificial flower after the first feeding bout, and the size of this flower was reduced to 2 cm by the end of training. All training was conducted near the end of the light portion of the moth light:dark cycle.

The wind tunnel working section dimensions were 119 × 61 × 61 cm with an octagonal cross section and a fan configuration permitting a maximum speed of 5.0 m s^{-1}, additional information on this tunnel is published elsewhere (Ortega-Jimenez et al., 2013). During training, the size of the artificial flower was reduced to one with a 2 cm diameter to minimize the aerodynamic profile of the flower and associated flow disruption. The effect of the flower on the drag experienced by the moth was also quantified, see below. In total, we recorded from 14 moths of body mass 1.295 ± 0.224 (mean ± s.d.) grams.

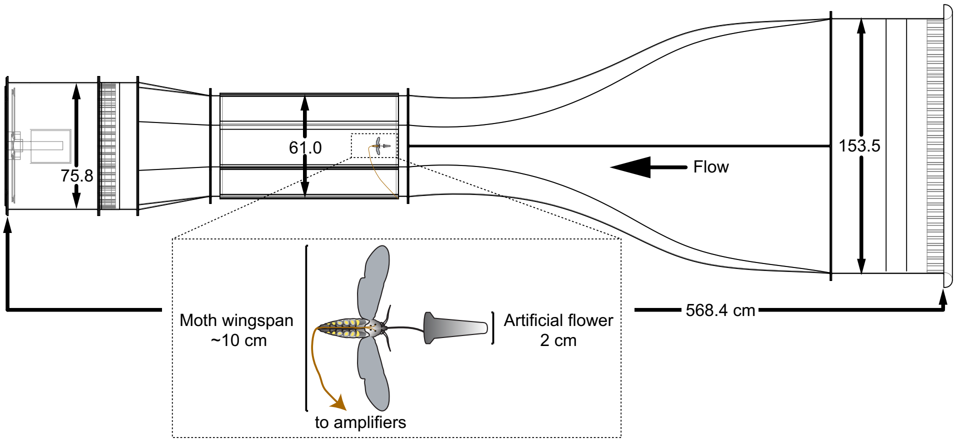

Fig. 2. An overhead view of the wind tunnel with moth and artificial flower shown to scale and enlarged in an inset. The artificial flower was positioned at the front of the working section centered in the horizontal and vertical axes. Recording electrode wires ran from their attachment point at the tip of the abdomen to an upper corner at the front of the wind tunnel working section and from there to the amplifiers.