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Current Opinion in Neurobiology

Neurobiology and biomechanics of flight in miniature insects

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Miniature insects can be as small as a few hundred micrometres in size, making them among the smallest metazoan animals ever described. Yet, even at these length scales, they display remarkably sophisticated flight behaviours. For flight at such low Reynolds numbers, miniature insects have evolved biomechanical and neural adaptations that push the boundaries of what is possible in the realm of physics and neurobiology of flight. After several decades of relative dormancy, this question has recently been revisited by researchers working in diverse areas ranging from systematics and neurobiology to dispersal behaviours. In this review, I cover recent findings in this area, and point towards the many open questions that still remain unanswered.

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Current Opinion in Neurobiology 2016, **41**:158–166

This review comes from a themed issue on **Microcircuit computation and evolution**

Edited by **Thomas R Clandinin** and **Eve Marder**

For a complete overview see the Issue and the Editorial

Available online 4th October 2016

http://dx.doi.org/10.1016/j.conb.2016.09.008

0959-4388/

Introduction

The body size distribution of the vast majority of insects is skewed towards length scales of no more than a few millimetres [1,2•]. Yet, much of what we know about the neural, physiological and biomechanical mechanisms of insect flight is derived from detailed studies on insect models such as locusts (e.g. [3]), flies (e.g. [4]), honeybees (e.g. [5]) and hawkmoths (e.g. [6]), which are an order of magnitude larger in size. Even the fruit fly *Drosophila*, with wingspan of approximately 5 mm, far exceeds various Phorid and Scatopsid flies in size. Entire families of certain insects (e.g. Trichogrammatid (chalcid) or Tinkerbella (fairyfly) wasps, Thysanoptera (thrips), and so on) are under 1 mm in size. In fact, these are among the smallest multi-cellular animals ever described, possibly reflecting global size constraints in metazoan taxa.

Sizes within single insect orders are also broadly distributed, for example, Hymenoptera range from 0.15 to 50 mm, Diptera from 0.4 to 85 mm, Odonata from 15 to 190 mm and Lepidoptera from 3 to 300 mm, and so on. Yet, over length scales of 2–3 orders of magnitude, these insects maintain flight-capability (Table 1). How do body morphologies and nervous systems of insects, and their flight ability in particular, cope with such extreme reduction in size? To address this question, we require knowledge of both the physical and physiological challenges posed by miniaturization. Among earliest papers on this topic was written by Rensch [7] in 1948, when the understanding of both neurobiology and biomechanics of flight in insects was quite rudimentary. Recent strides in physics to physiology of flight have led to a renewed interest and research in miniature insects, which is summarized in comprehensive reviews by Polilov [8••] on the anatomy and natural history, and by Chittka, Niven and colleagues [9,10••] on aspects of neuronal computation. This review focuses specifically on flight mechanisms of insects in sub-millimeter size range.

Biomechanical limitations of size

For miniature insects, moving in air presents a formidable challenge. Insects ranging from 0.2 to 1 mm size typically operate at Reynolds numbers (hereafter Re, the ratio of inertial to viscous forces on wings, calculated as $Re = 2\varphi n R^2/v$; where φ is the wing amplitude (radians), n is the wingbeat frequency, R is the characteristic wing length, and ν is the kinematic viscosity of air at 27 C) of 1–100 (e.g., *Thrips* spp. ($Re < 10$; [11]), *Trichogramma* spp. ($Re < 10$), or the chalcid wasp, *Encarsia formosa* ($Re \sim 20$; [12]). In this range of Re, there is significant viscous dissipation of the kinetic energy imparted by wings to the surrounding fluid [13]. Such insects must flap continually to stay aloft, because the lack of inertia means that they instantly cease to move when they stop flapping. This also places the requirement for additional energetic investment in face of already diminished storage ability.

Viscous losses can be mitigated via wing kinematics and morphological adaptations. For example, enhancing wingbeat frequencies and amplitudes can ensure an overall increase in Re. Most holometabolous insects modulate flight forces by controlling their wingbeat amplitude rather than frequency, which is constrained by their fixed musculo-thoracic architecture. Miniature insects fly with nearly maximal wing amplitudes, a natural consequence of which is the occurrence of 'clap-and-fling' in which both wings *clap* at the end of upstroke, and peel off and

Table 1

Typical size ranges in the major insect orders. This table showcases the most extreme examples of small and large sizes within each order based on available literature. In these publications, size is not measured or reported in a consistent manner. In some cases, it is reported in terms of wing span and/or body length. Although wherever possible, the most extreme (smallest or largest) sizes are included, these data are subject to change as new discoveries are made. Hence, these examples presented here should be treated as typical exemplars for small or large sized members of each group, rather than the most extreme. WS, wing span; BL, body length.

	Smallest reported size*		Largest reported size* (species)	
Pterygote order	Common name *Species name*	Smallest reported size*	Common name	Largest reported size*
Odonata	Scarlet Dwarf, Northern Pygmyfly, or Tiny Dragonfly *Nannophya pygmaea* (Anisoptera: Libellulidae) [42]	BL = 16 mm WS = 30 mm	Giant Hawker *Tetracanthagyna plagiata* (Anisoptera: Aeshnidae) Griffinfly *Meganeuropsis permiana* (extinct) (Protoanisoptera:Meganeuridae) [43]	BL = 100 mm WS = 123–145 mm WS = 640 mm
	Wisps (Damselflies) *Agriocnemis* spp. (Zygoptera:Coenagrionidae) e.g.[44]	BL ~ 20 mm WS ~ 20 mm	Forest Giants *Megaloprepus coerulatus* (Zygoptera: Pseudostigmatidae) [45]	WS = 190 mm
Orthoptera	Ant-inquiline crickets *Myrmecophilus acervorum* (Ensifera:Myrmecophilidae) [46]	BL = 2 mm Flightless	Northern Arboreal Giant Weta, Wetapunga *Deinacrida heteracantha* *(Orthoptera: Henicidae)*	BL = 82 mm Flightless
Hemiptera	Pirate bugs *Xylocorus flavipes* (Hemiptera: Anthocoridae)	WS = 2–3 mm BL = 1.5–2 mm.	Giant Waterbug *Lethocerus americanus* (Hemiptera: Belostomatidae) Empress Cicada *Megapomponia imperatorial* (Hemiptera: Cicadidae)	BL = 40–60 mm WS = 117 mm WS = 180–200 mm BL = 70 mm
Blattoidea	Termites *Serritermes sermfer* (Blattoidea: Isoptera) [47]	BL = 4 mm WS = 8–9 mm	Giant Northern termite *Mastotermes darwiniensis* (Blattoidea: Isoptera) [48] *Gyatermes styriensis* (extinct) [49]	BL = 110 mm (queen) BL = 36 mm (workers) Flightless WS = 76 mm BL = 25 mm
	Ant Cockroaches *Attaphila fungicola* (Blattoidea: Blattellidae) [50]	BL = 3–5 mm	Central American giant cave cockroach *Blaberus giganteus* (Blattoidea: blaberidae)	WS ~ 150 mm BL ~ 100 mm
Thysanoptera	Thunderflies, Storm flies, corn lice thrips,	BL = 0.5 mm	Spore-feeding Thrips *Idolothrips marginatus* (Thysanoptera:Phlaeothripidae)	BL = 14 mm
Strepsiptera	Twisted-wing parasites [51] *Elenchus* (Strepsiptera: Elenchidae)	BL = 1.5 mm WS = 2.5 mm	*Mengenilla*. (Strepsiptera: Mengenillidae) *Protoxenos janzeni* *(extinct)*	BL = 5.7 mm W = 3.5 mm BL = 7.6 mm
Neuroptera	Dustyflies (Neuroptera: Coniopterygidae)	WS ~ 6–10 mm	Dobsonflies (Megaloptera: Corydalidae) [52]	 WS = 180 mm BL ~ 75 mm
Hymenoptera	Fairyfly wasps *Kikiki Huna* (Hymenoptera: Mymaridae)	WS = 0.19–0.30 mm	Asian Giant Hornet *Vespa mandarinia*	WS = 75 mm
	Mining bees *Perdita minima* (Hymenoptera: Andrenidae)	BL = 2 mm	Wallace's Giant Bee *Megachile pluto*	WS 63.5 mm
	Pharaoh Ants *Monomorium pharaonis* (Hymenoptera: Formicidae)		Giant Amazonian Ants *Dinoponera Gigantea*	BL = 30–40 mm Wingless