JℳPAPERS

Wing–antenna interaction reduces odour fatigue in butterfly odour-tracking flight

Zhipeng Lou[1], **Menglong Lei**[1], **Haibo Dong**[2] **and Chengyu Li**[1],†

[1]Department of Mechanical & Aerospace Engineering, Case Western Reserve University, OH 44106, USA

[2]Department of Mechanical & Aerospace Engineering, University of Virginia, Charlottesville, VA 22903, USA

Flying insects exhibit remarkable capabilities in coordinating their olfactory sensory system and flapping wings during odour plume-tracking flights. While observations have indicated that their flapping wing motion can 'sniff' up the incoming plumes for better odour sampling range, how flapping motion impacts the odour concentration field around the antennae is unknown. Here, we reconstruct the body and wing kinematics of a forwards-flying butterfly based on high-speed images. Using an in-house computational fluid dynamics solver, we simulate the unsteady flow field and odourant transport process by solving the Navier–Stokes and odourant advection-diffusion equations. Our results show that, during flapping flight, the interaction between wing leading-edge vortices and antenna vortices strengthens the circulation of antenna vortices by over two-fold compared with cases without flapping motion, leading to a significant increase in odour intensity fluctuation along the antennae. Specifically, the interaction between the wings and antennae amplifies odour intensity fluctuations on the antennae by up to 8.4 fold. This enhancement is critical in preventing odour fatigue during odour-tracking flights. Further analysis reveals that this interaction is influenced by the inter-antennal angle. Adjusting this angle allows insects to balance between resistance to odour fatigue and the breadth of odour sampling. Narrower inter-antennal angles enhance fatigue resistance, while wider angles extend the sampling range but reduce resistance. Additionally, our findings suggest that while the flexibility of the wings and the thorax's pitching motion in butterflies do influence odour fluctuation, their impact is relatively secondary to that of the wing–antenna interaction.

Key words: swimming/flying

† Email address for correspondence: cxl1692@case.edu

1. Introduction

Flying insects, as products of natural engineering, are tiny yet equipped with advanced features: highly efficient flapping wings (Heinrich 1974; Lehmann, Dickinson & Patel 1997; Jones & Babinsky 2012; Lehmann, Wang & Engels 2021), robust flight control (Fry, Sayaman & Dickinson 2003; Iwamoto & Yagi 2013; Dickinson & Muijres 2016; Farisenkov *et al.* 2022) and sophisticated sensory neural networks (Taylor & Krapp 2007; Rapp & Nawrot 2020; Tuckman *et al.* 2021). The collaboration of these features allows insects to precisely navigate in a complex flow environment. To gain inspiration on artificial insect-like systems, scientists endeavour to understand these complex mechanisms of collaborations (Ashley & Rodden 1972; Lehmann, Sane & Dickinson 2005; Ruiz & Theobald 2020; Hürkey *et al.* 2023). While insects are managed to coordinate these functions for complex tasks, current man-made designs are facing challenges in integrating these features. For example, even equipped with highly sensitive sensors, rotary drones have trouble detecting chemicals because of the strong induced flow in downwash, which blows away most of the chemicals (Allers *et al.* 2023). This limitation makes odour-detection drones ineffective and even dangerous to work at places where hazardous chemicals have risks of spreading out. In contrast, insects have a fundamental ability of not blowing away these chemicals, especially when odour detection is the main purpose of the flight, such as during foraging or mating. Compared with current drone designs, insects stroke their flapping wings to keep aloft instead of rotary blades. Understanding the mechanism of how insects coordinate their wing flapping motion and olfactory perception is necessary for replicating the chemical detection performance in designs of unmanned devices navigating in dynamic flow environments.

1.1. *Olfactory sensory and flying are not conflicting for insects*

Olfactory sensory while flying is an essential ability of insects which is crucial for foraging, mating, and communication (Baker 1989; Baker *et al.* 2018; Lin 2023). However, during an odour plume-tracking flight, the flapping motion of insects' wings inevitably disturbs the surrounding air due to the generation of wing-induced flow. The disturbance of the flow field can potentially blow away the incoming odour plume, causing the failure of odour sensory, just like the failure of rotary drones for odour detection. Recent research has shown that when insects fly under a high reduced frequency, the induced flow redirects the plume to flow above the antennae by forming a shield-like streamline in the frontal flow field (Lei & Li 2023). It is true that such induced flow reduces the plume reachable by antennae, which has a negative effect on odour perception. However, this shielding effect serves other benefits – increasing the odour sampling range. This is desirable when insects are flying in the mode called cross-wind zigzagging – a flight mode when the insects need larger sampling due to lost odour clues. This active motion can be analogous to 'sniffing' in mammals (Tripathy *et al.* 2010). Conversely, during an upwind surging flight – the other mode that requires stable track of odour clue – insects prioritize strengthening peak odour intensity over antennae, sacrificing the odour sampling range. Evaluating the odour intensity over the antennae of fruit flies during forwards flights, Li, Dong & Zhao (2018) reported that the wing-induced flow enhances the peak odour flux over the antennae up to 1.8 times. By switching wing kinematics between two flight modes, insects can strategically track the odour source. This adaptability enables insects to locate odour sources in complex environments with obstacles, weak odour fields and natural disturbance (Wolf 2011; Conchou *et al.* 2019; Lei & Li 2023).

1.2. *Olfactory adaptation*

In addition to the ability to 'sniffing' odourants without dispersing them, insects still have a weakness that is shared with mammals: continuous odour stimulus will lead to olfactory adaptation, commonly known as odour fatigue. Unlike artificial odour sensors (Wen *et al.* 2018), insects' sensilla neurons can reach an adapted state under continuous stimuli (Dolzer, Fischer & Stengl 2003). Experimental observations have revealed that moths show a better response to pulsatile odour delivery compared with constant odour stimuli (Baker *et al.* 1985; Dolzer *et al.* 2003; Daly *et al.* 2013). However, under steady odour delivery, moths have poor sensory performance. Sanders (1997) conducted an experiment where a moth is navigating in a high-concentration field of pheromone, and it loses track of the pheromone source. The main reason for the failure is that the stimuli intensity is so much stronger than in a natural environment that the moth senses a relatively constant odour intensity that causes odour fatigue.

In nature, to locate odour sources in complex environments, insects must have mastered some mechanisms that help them overcome odour fatigue. For example, as insects swarm – a mating and pairing activity for many insects (Syrjämäki 1964; Sullivan 1981) – insects must have a way to track the pheromone plume under continuous pheromone stimuli without getting odour fatigue. We hypothesize that insects' ability to navigate in such concentrated pheromone fields may be the result of the beneficial flapping motion. Several experiments have shown some hints that induced airflow, a byproduct of flapping flight, varies linearly with wing beat frequency and alters the olfactory stimuli received by the sensory organs (Sane 2006; Sane & Jacobson 2006). This induced airflow potentially creates fluctuations, preventing the sensory neurons from reaching an adapted state. However, to date, there is a lack of comprehensive explanation that attributes the mechanism of the odour fatigue resistance to the flapping motion, especially from a fluid mechanic perspective.

1.3. *Wing-induced flow on olfactory perception*

During flight, the existence of antennae and wing-induced flow have a mutual influence: the structure of antennae may disturb the induced flow, while flow affects sensory perception. For example, much research found that the rami density of pectinate antennae (comb-like structure) among insects, like moths, effectively affects how much the air can flow through the sensilla, influencing the pheromone capture (Jaffar-Bandjee *et al.* 2020*a*,*b*). In contrast, the wing-induced airflow can decrease the depth of the velocity boundary layer over antennae and thereby increase the rate of interception of air-born olfactory cues by at least an order of magnitude (Loudon & Koehl 2000; Loudon & Davis 2005). Although current researchers have noticed the antennae themselves may affect the flow, most research still only treats the antennae of insects as proprioceptors, providing speed feedback to insects (Roy Khurana & Sane 2016). The inter-antennal angle, the angle between two antennae, is used to estimate the airspeed in experiments (Schneider 1964).

Recent research has observed that when insects land on odour sources, they actively vibrate their antennae to enhance sensory sampling (Schneider 1964; Loudon 2009; Dürr, Berendes & Strube-Bloss 2022). We speculate that this antennal movement can induce fluctuations in the air, affecting the distribution of odour plumes. Such fluctuations are crucial for preventing odour fatigue, particularly as insects land on odour sources. However, insects exhibit different behaviour during flight, where antennae remain relatively fixed at certain angles to maintain flight stability (Krishnan *et al.* 2012). Frequent movement of antennae may break the balance of inertial forces, making the flight unstable.

Thus, aside from the benefits of antennal movements, odour fatigue resistance may also be attributed to the induced flow from wing flapping motion, termed wing–antenna interaction. Considering that the induced flow has been found to provide some benefits for odour perception, flapping motion can serve as an alternative to antennal movement during flight.

1.4. *Other impact factors: body motion and wing flexibility*

Many factors can influence the odour perception of antennae, potentially mitigating odour fatigue. One such factor is body motion. Based on observations, some insects exhibit periodic body rotations during odour-tracking flights. The oscillation of the butterfly's body has been found to actively influence the direction of vortex rings generated by flapping wings (Fei & Yang 2016) and enhance aerodynamic performance (Chang *et al.* 2020). As antennae are fixed on the head during the flight for balance purposes, body motion leads to relative antennal motion against the global coordinates. When the antennae intersect the air flow, corresponding air disturbances may generate fluctuations in the odour field, potentially preventing odour fatigue. However, the specific impact of body motion on odour perception remains unexplored.

Another factor is wing flexibility. In contrast to rigid wings, the deformation of flexible wings facilitates the transfer of wing momentum to the wake, directing a more effective direction of aerodynamic forces according to the flight direction (Young *et al.* 2009). This ability to direct airflow backwards during forwards flight potentially mitigates backflow that disperses incoming plumes. However, further investigation is required to confirm this speculation as the impacts of other aforementioned factors are explored.

1.5. *Modelling the free-flying butterfly and numerical simulations*

Butterflies offer a unique opportunity to study both flight aerodynamics and olfactory sensing. Their signature long antennae allow easier analysis of flow dynamics and potential interactions with wings due to the relatively low ratio between antenna length and wingspan. Compared with other species such as moths and locusts, butterflies typically have low-aspect-ratio wings, with aspect ratios (ARs) ranging from 1.5 to 2.5 (Betts & Wootton 1988; Dudley & Srygley 1994; Tanaka & Shimoyama 2010). Compared with high-aspect-ratio wings ($AR > 3$) of other insects, flapping wings under low AR results in stronger wingtip vortices and increased air perturbation, facilitating clearer observations of wing-induced flow (Le Roy, Debat & Llaurens 2019). Additionally, butterflies commonly use a combination of thorax-pithing and abdominal oscillation with wing flapping, setting them apart from other insects. Furthermore, the aerodynamic effects of wing deformation in butterflies are well-studied due to their relatively higher wing flexibility, allowing for a more focused investigation of its impact on olfactory performance.

To address our speculations, we first reconstructed the kinematics of flapping wings and oscillating bodies based on high-speed videos of forwards-flying butterflies. We specifically selected an upwind surging butterfly for analysis to simplify the investigation by excluding complex flight manoeuvres during zigzagging flights. Employing an in-house high-fidelity computational fluid dynamics (CFD) solver, we explored the unsteady flow field and odourant transport process by solving both the Navier–Stokes and advection-diffusion equations.

A series of comprehensive parametric studies were conducted to investigate how or whether wing-induced flow resulting from wing-antenna interaction can prevent odour fatigue. Our aim was to address these questions from a fluid mechanics perspective:

Parameters	Values
Total mass, m (g)	0.60
Body mass, m_b (g)	0.48
Wing mass, m_w (g)	0.06
Wingspan length, R (mm)	44.90
Wing area, S_w (mm^2)	1151.09
Forewing area, S_f (mm^2)	641.87
Hindwing area, S_h (mm^2)	509.22
Wing loading, $mg/(2S_w)$ (N m^{-2})	2.56
Aspect ratio, $AR = R^2/S_w$	1.75
Flapping frequency, f_w (Hz)	11.11
Forwards flying speed, U_∞ (m s^{-1})	0.85

Table 1. Morphological parameters of the monarch butterfly (*Danaus plexippus*).
*The parameters in the table are listed for one side of the wings.

(i) how or whether wing-antenna interaction can prevent odour fatigue, (ii) how or whether inter-antennal angles can modulate the wing-antenna interaction mechanism, and (iii) what extent flexible wing pairs and varying thorax pithing contribute to odour fatigue resistance.

2. Methodology

2.1. *Reconstruction of freely flying butterfly*

Monarch butterflies (*Danaus plexippus*) were wild captured and expected to fly into a filming scene voluntarily. The filming scene consisted of three orthogonally calibrated high-speed video apparatus (Photron Fastcam SA3 60 K, Photron USA, Inc, San Diego, CA, USA) with a shutter speed of 1/(20 000) s and a resolution of 1024×1024 pixels. Three orthogonal whiteboards were set as backgrounds placed towards each camera. We collected approximately 20 separate recordings of free-flying butterflies at 1000 frames per second. One recording was selected when the butterfly was performing a forwards flying at a constant speed (0.85 m s^{-1}). The morphological parameters of the corresponding butterfly are summarized in table 1.

To reconstruct the freely flying butterfly, we adopted a template-based hierarchical subdivision surface method with joint controllers using Autodesk MAYA (Autodesk, San Raphael, CA, USA). Figure 1 compares the real butterfly with our model with a template mesh. Morphologically, a butterfly has a forewing and a hindwing on each side. During flight, the forewing and hindwing partially overlap with each other serving as a single lifting surface. To reduce computational complexity in CFD simulation, the forewing and the hindwing were modelled as one piece in the current study. A similar modelling approach has also been adopted in previous studies (Yokoyama *et al.* 2013; Zheng, Hedrick & Mittal 2013; Bode-Oke & Dong 2020). Figure 2(*a*) demonstrates the reconstruction process at a selected instant. The high-speed videos were loaded into the virtual cameras based on the experimental set-up. The wing and body kinematics were applied to the model according to the two-dimensional (2-D) images (figure 2*b*,*c*).

The surface of the model was controlled by a set of joint controllers of the template model. Each of the joints governs the nearby meshes. The relationship of the joints is established on a hierarchy of 'parent' and 'child', where parent joints control the child joint controllers. By rotating one joint against the centre of itself, for example, the
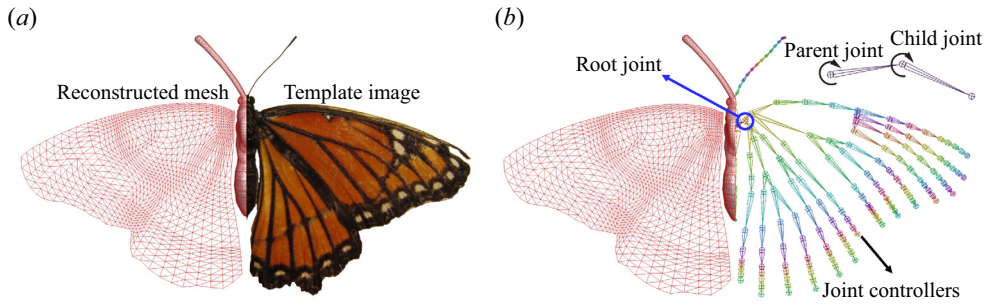
Figure 1. (*a*) Monarch butterfly (*Danaus plexippus*) with the computational model on the left half. (*b*) Schematic of the joint controllers for adjusting surface deformation.