Flight muscle timing, wing kinematics, and 3-dimensional body orientation of loosely tethered locusts responding to looming objects

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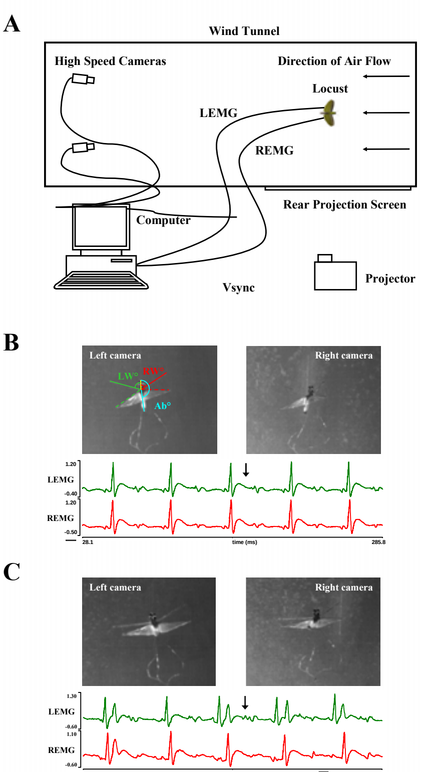
Introduction

In locust flight, collision avoidance behaviour involves integration of visual sensory cues with coordinated, bilateral, wing muscle activity. Previous studies examining wing and body kinematics used open loop conditions that prevented generation of realistic steering torques in all three rotational degrees of freedom (yaw, pitch, and roll). Recently, motor neuron activity in rigidly tethered locusts has been related to the initiation of a glide as a last ditch avoidance manoeuvre (Santer et al. 2005). Collision avoidance responses of loosely tethered locusts, however, suggest that this behaviour is more complicated and subtle than previously thought (Mohr and Gray 2003). We recorded 3D flight behaviour, wing kinematics, and depressor muscle activity from loosely tethered locusts presented with looming stimuli to examine mechanisms of collision avoidance behaviour in minimally restricted animals.

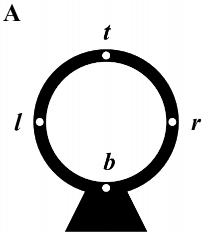
1 Setup and recording



A) Wind tunnel and recording set up. B) Concurrent video and EMG (m97) data during straight flight. Phase-locked EMG spikes correspond to forewing symmetry at the start of the downstroke. C) Concurrent video and EMG data during the start of a left turn. Earlier LEMG spikes correspond to greater depression of the left wing at the start of the downstroke. Forewing asymmetry (FWA) = LW° - RW°. Abdomen angle (Ab°) was normalized to 180°. Arrows indicate the time of the video frames.

2 Sample data

A

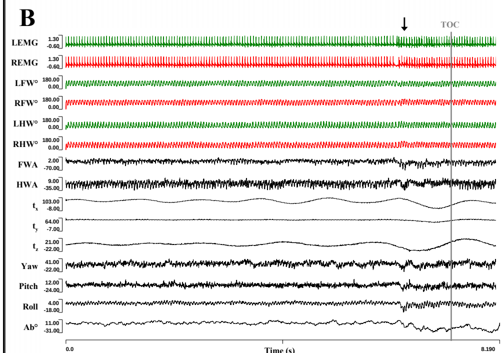


$$Yaw = \tan^{-1}\left(\frac{r_z - l_z}{l_x - r_x}\right)$$

$$Pitch = \tan^{-1}\left(\frac{t_z - b_z}{t_y - b_y}\right)$$

$$Roll = \tan^{-1}\left(\frac{b_x - t_x}{t_y - b_y}\right)$$

B



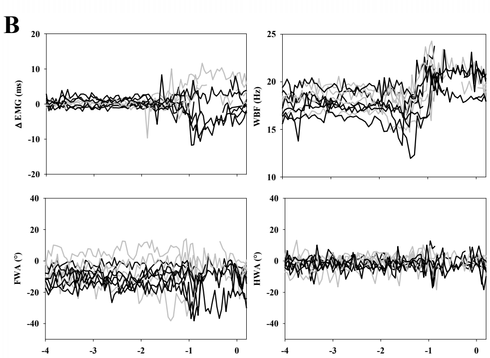
A) Tether marks and equations to calculate rotation angles in 3D space, using appropriate x, y, and/or z coordinates of the top (t), bottom (b), left (l), and right (r) marks. Angles were calculated relative to the normal for each plane. B) Concurrent EMG, kinematic, and orientation data for one approach. Only the top tether coordinates are shown. There are apparent changes in the wing asymmetries as well as pitch, roll, and abdomen angles 1 s (arrow) before time of projected collision (TOC).

3 Behaviour , Kinematics

A

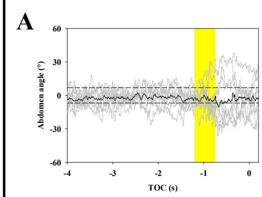
Response	Turn Left	Turn Right	Glide	Stop	No Response
Animal					
1	1 (-1.208)				
2	2 (-0.511)		1 (-1.939)		
3		1 (-0.968)			
4	3 (-0.880)		1 (-1.676), 2 (-1.204)		
5	1 (-0.892)				
6	3 (-0.764)		1 (-2.164), 2 (-1.492)		
7		1 (-0.873)			
8		1 (-1.217)			
9	1 (-0.956)				
10	1 (-0.979)				
11		1 (-1.104)			
12			1 (-1.081)	2 (-0.969)	
13	3 (-0.863)		1 (-1.503)	2 (-1.343)	
14					1
15		2 (-0.825)	1 (-1.197)		
16		2 (-0.941)	1 (-1.569)		
17	1 (-0.847)				
18	1 (-0.842)				
Total	6/10	4/6	7/9	0/2	1/1

B



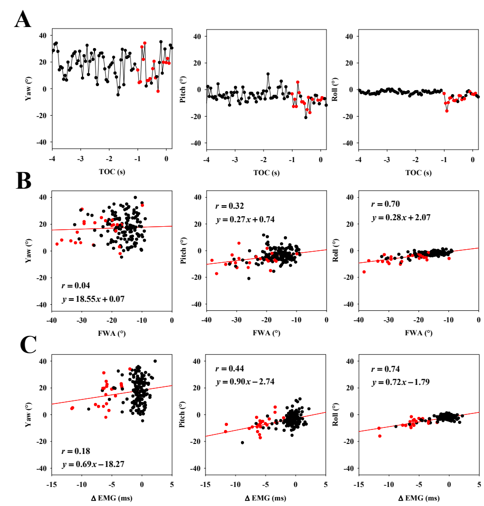
A) Response categories of each animal and the timing (in brackets) relative to TOC. First responses are highlighted in yellow, multiple responses are numbered sequentially. B) Change in EMG timing (Δ EMG $= t_{LEMG} - t_{REMG}$), wingbeat frequency (WBF), FWA, and HWA relative to TOC. Data were selected from trials in which the first response was a turn to the left (black) or right (grey).

4 Abdomen angle



A) Abdomen movement was not associated with initiation of turning behaviour. The mean abdomen angle (black line) was calculated from all animals that turned (grey lines, n=10). Dashed lines represent upper and lower 95% confidence intervals of the mean trace. Yellow represents the range of times that turning began.

5 Δ EMG and FWA predict roll



Orientation, kinematics, and muscle activity during a turn to the left. A) During an approach, yaw and pitch were variable, whereas the roll angle was more consistent and showed a clear shift to the left 1 s before TOC. FWA (B) and Δ EMG (C) were most strongly correlated with the roll angle. Black symbols are from single left EMG spikes, red symbols are from double left EMG spikes. r is the Pearson correlation coefficient and the equations describe the linear regressions (red lines).

Summary/Conclusions

- Looming stimuli evoke 3D steering and gliding behaviours in loosely tethered locusts.
- Steering involves changes in muscle timing, FWA, and WBF.
- Abdominal ruddering is not involved in the initiation of a turn.
- Bilateral M97 activity and FWA predict changes in the roll angle during a turn.

References

Santer et al. (2005) *J. Comp. Physiol. A* 191:61-73; Mohr and Gray (2003) *Neurosci. Abstr.* Program number 403.20.

Acknowledgements

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