Control errors during the hold phase of head-bobbing in pigeons

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INTRODUCTION

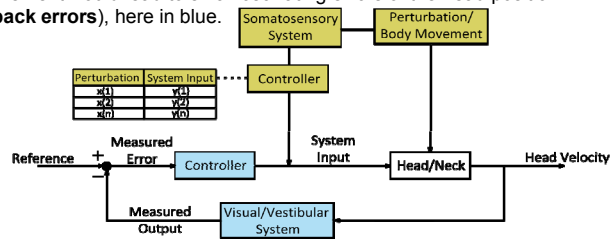
Walking pigeons display a head-bobbing behaviour with two alternating phases. During the hold phase the head is kept motionless in space, while during the thrust phase the head is thrust forward to keep up with the constantly moving body. In order to maintain a stationary head position in space, the head has to compensate for the constant body movement during the hold phase .

Which systems control head movement during the hold phase?

Two possibilities are:

a.) Body perturbation (movement) is measured directly and a correction is performed based on previously learned 'look-up table'. Calibration errors in this 'look-up table' would lead to small but constant deviation (**prediction errors**) of the optimal head position. (yellow)

b.) Head movement is measured and deviations from the reference are corrected for based on this measurement. Processing time of each measurement would lead to small oscillating errors of the head position (**feedback errors**), here in blue.

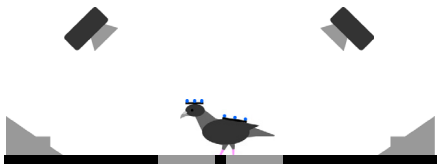


We analysed kinematic data from head and body and characterized the control errors during the hold phase. Small hold phase speeds indicate prediction control, whereas small oscillatory movements indicate feedback control.

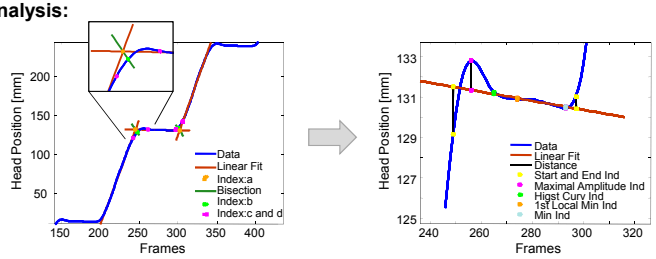
METHOD

Animals:
- 4 pigeons

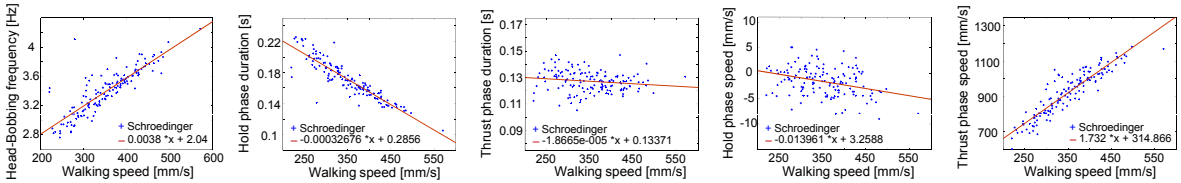
Setup:
- 4 motion capture cameras
- 360 Hz sampling frequency
- Reflective markers
- 2 feeders between the pigeons walked
- Static sinusoidal lumination grid (black and white stripes)



Analysis:

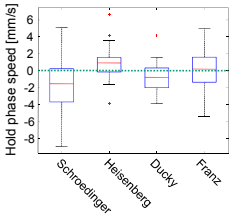


RESULTS



General walking features

- As pigeons walk faster the head-bobbing frequency increases linearly (0.0038 Hz/(mm/s)).
- The **hold phase** duration decreases with increasing walking speed (-0.00033 s/(mm/s)). Head speed remains almost constant (~ -1.65 mm/s)
- The **thrust phase** duration remains constant with increasing walking speed (mean: 0.127 s/(mm/s)). The head speed increases with 1.7297 (mm/s)/(mm/s).

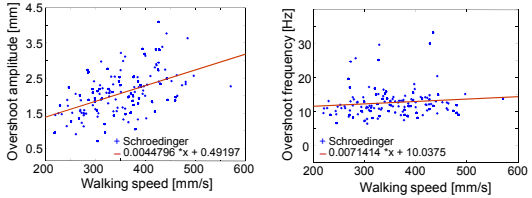


Prediction errors?

- The hold phase speed does not systematically differ from the expected speed of 0 mm/sec between the measured birds.
- Schroedinger and Heisenberg: significant deviation from speed zero ($p<0.05$).

Feedback errors?

- A small and consistent oscillation in the phase transition was found.
- The phase transition amplitude increases 0.0044 mm per mm/s walking speed.
- The **oscillation frequency** is constant (~12.9 Hz) over walking speed.



Compiled data – all 4 pigeons

ID	Slopes of the linear fit (always agaist walking speed)					Overshoot Amplitude		Overshoot Frequency	
	HB-freq.	Hold phase duration	Thrust phase duration	Hold phase speed	Thrust phase speed	Slope	Mean	Slope	Mean
Schroedinger	0.0038	- 0.00033	- 0.000019	- 0.014	1.729	0.0044	2.07	0.0071	12.85
Ducky	0.0048	- 0.00037	- 0.000081	0.0074	2.430	0.0076	1.94	- 0.0037	14.22
Franz	0.0037	- 0.00029	0.0000032	0.0040	1.655	0.0002	1.30	- 0.015	15.22
Heisenberg	0.00068	- 0.000058	0.000025	0.0092	0.82	0.00043	1.20	0.0074	15.43

SUMMARY & DISCUSSION

General walking features

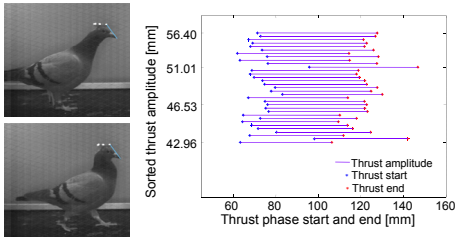
When increasing the walking speed:
- Hold phase duration is reduced, but not its features.
- Thrust phase duration is not reduced; it increases in speed.
  - Therefore the head-bobbing frequency and the thrust amplitude increases, leading to a faster overall head movement.

Prediction errors

- There is no systematic head speed deviation from zero between birds, but significant individual deviation
  → Data suggests individual internal 'look-up table'

Feedback errors

- The oscillatory movement indicate the response of a sensory feed back control system.
- The head-bobbing amplitude increases slightly with walking speed, demonstrating more perturbation in processing time
- Thrust start and end can vary
  → sensory control, not mechanical.
- Marker movement can also be excluded.



REFERENCES

1. Troje, N. F. & Frost, B. j. (2000). Head-Bobbing in Pigeons: How stable is the Hold Phase? Journal of experimental Biology, 203, 935-940.

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