Active sensation and spatiotemporal remapping in olfaction and vision: parallels and contrasts

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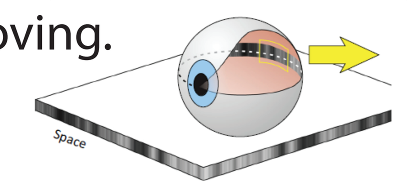
Introduction

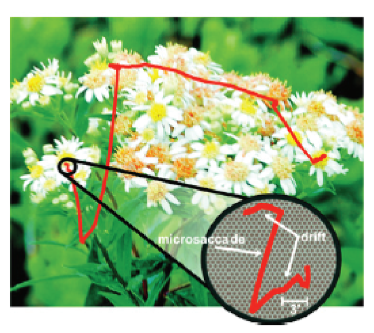
A main goal of sensory systems is to extract behaviorally-relevant information from the physical signals impinging on their receptors. Objects are often static, but – typically due to biophysical constraints – receptors respond better to fluctuating signals than to constant ones. In many sensory systems, active sensation can transform static signals into dynamic ones. In olfaction, the dynamics of plumes can also carry out this transformation. Here, we develop a common analytic framework to analyze these transformations. We then use this framework to compare the way that these two processes affect the dynamics of sensory inputs.

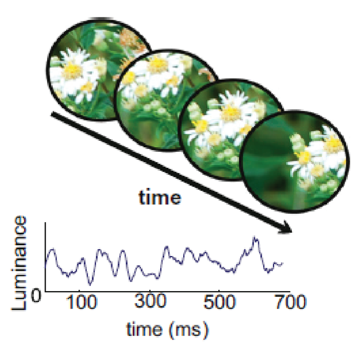
Active Sensation

Eye Movements

During natural viewing, the eyes are constantly moving.



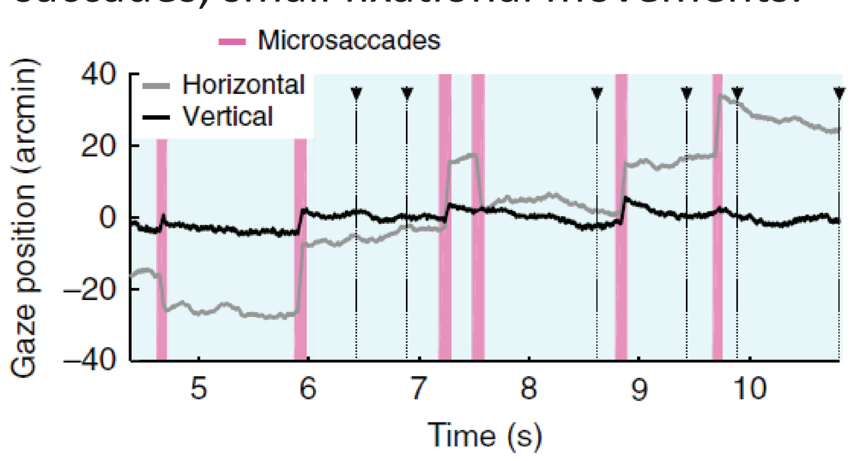




Rucci, M., & Victor, J. D. (2015). The unsteady eye: an information-processing stage, not a bug. TINS, 38(4), 195-206.

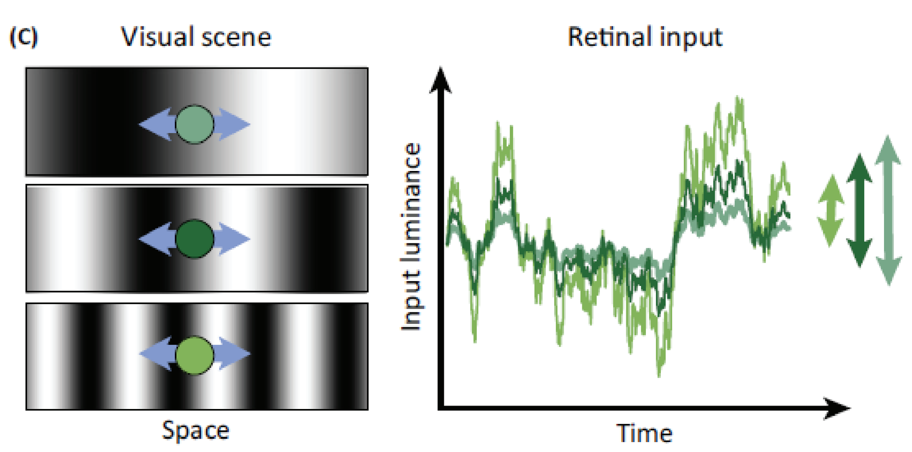
Kuang, X., Poletti, M., Victor, J. D., & Rucci, M. (2012). Temporal encoding of spatial information during active visual fixation. Current Biology, 22(6), 510-514.

These movements consist of rapid saccades and, between the saccades, small fixational movements.



Intoy, J., & Rucci, M. (2020). Finely tuned eye movements enhance visual acuity. Nature Communications, 11(1), 795.

The fixational movements are approximately Brownian and move a point in the image across dozens of photoreceptors.

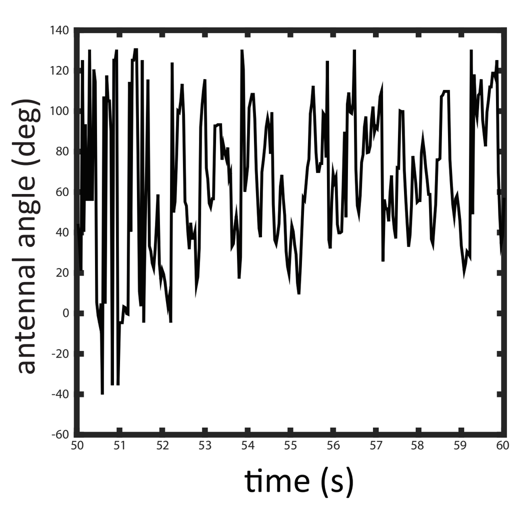


Rucci, M., & Victor, J. D. (2015). The unsteady eye: an information-processing stage, not a bug. TINS, 38(4), 195-206.

Motion of the receptors induces temporal transients, and the statistics of these transients depend on the spatial characteristics of the sensory input.

Antennal Movements

Antennal movements are prominent in insects and, in many insects, may be analogous to eye movements. This recording (H. Lei, unpublished data) shows the angular position of a honey bee's right antenna in the absence of an olfactory stimulus.



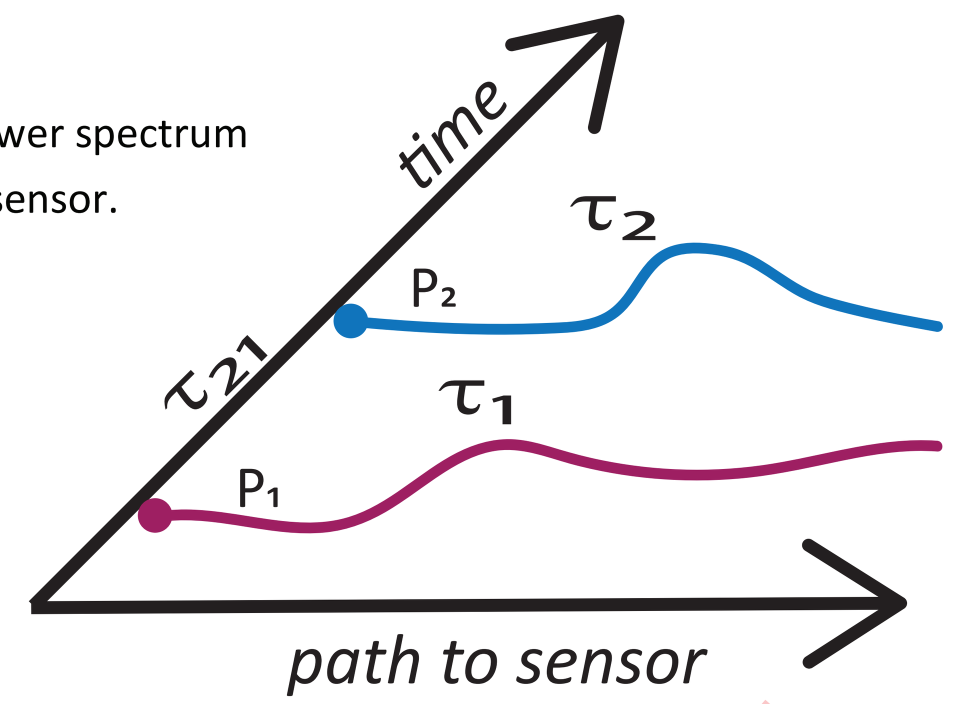
How flows and sensor movement modulate olfactory signals

Analysis

$a(\tau)$: the probability that a stimulus particle that leaves the source at time t arrives at the sensor at time $t+\tau$

$b(\tau_1,\tau_2,\tau_{21})$: the joint probability that a stimulus particle that leaves the source at time t_1 arrives at the sensor at time $t_1+\tau_1$, and that a second particle that leaves the source at time t_2 arrives at the sensor at time $t_2+\tau_2$.

The times of emission are separated by $\tau_{21}=t_2-t_1$



The Fourier transform of $b(\tau_1,\tau_2,\tau_{21})$ determines how the power spectrum at the source is transformed into the power spectrum at the sensor. Specifically, with

$$b(\omega_1,\omega_2,\lambda)=\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} b(\tau_1,\tau_2,\tau_{21})e^{-i\omega_1\tau_1-i\omega_2\tau_2-i\lambda\tau_{21}}d\tau_1 d\tau_2 d\tau_{21},$$

the power spectra of the odor concentration at the source and the sensor are related by

$$P_{sensor}(\omega_{out})=\frac{1}{2\pi}\int_{-\infty}^{\infty}P_{source}(\omega_{in})b(\omega_{out},-\omega_{out},\omega_{in}-\omega_{out})d\omega_{in}.$$

Active Sensing

With active sensation but no transport delay, $b(\tau_1,\tau_2,\tau_{21})=\delta(\tau_1)\delta(\tau_2)q(\tau_{21})$, where q is the autocorrelation of sensor motion.

In this case, $\tilde{b}(\omega_1,\omega_2,\lambda)=\tilde{q}(\lambda)$ and

$$P_{sensor}(\omega_{out})=\frac{1}{2\pi}\int_{-\infty}^{\infty}P_{source}(\omega_{in})\tilde{q}(\omega_{in}-\omega_{out})d\omega_{in}.$$

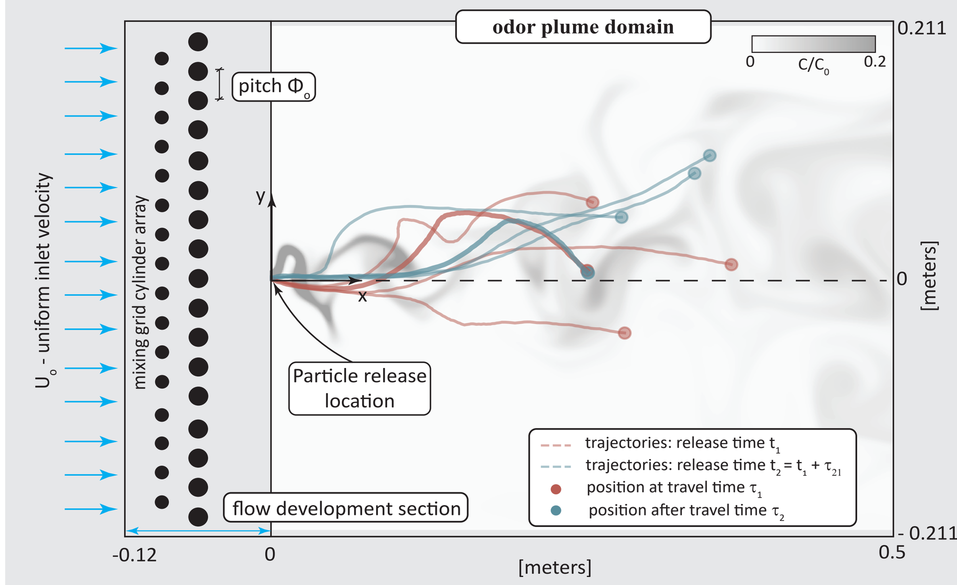
Consequently, the output can contain frequencies that are not present in the input. This frequency-spreading is characterized by a convolution.

Laminar Flow

In purely laminar flow, particles diffuse independently. In this case, $b(\tau_1,\tau_2,\tau_{21})=a(\tau_1)a(\tau_2)$ and $\tilde{b}(\omega_1,\omega_2,\lambda)=2\pi\tilde{a}(\omega_1)\tilde{a}(\omega_2)\delta(\lambda)$, so $P_{sensor}(\omega)=P_{source}(\omega)\left|\tilde{a}(\omega)\right|^2$.

Each input frequency component is transferred to an output component at the same frequency, although its amplitude may be changed. That is, there is filtering but no frequency spreading.

Computational Fluid Dynamics



Schematic of simulation setup. First, a 2D velocity field representing grid turbulence was generated using a finite element model (generated in Tootoonian et al., in review). The gray shading shows an example snapshot of a concentration field modeled for an odor source located near the origin, to provide a sense of the plume extent and the coherent structures present in the velocity field. Massless tracer particles were then released at the origin at various time intervals and transported using the velocity field and a stochastic diffusion process. Example particle trajectories are plotted at t = 23.06s for two different release times - the red particles at t_1 = 20.6s (travel time τ_1 = 2.46s) and the blue particles at t_2 = 20.7s (travel time τ_2 = 2.36s). Note that while particles released at the same time tend to be more correlated than particles released at different times, even particles released at the same time can become separated due to diffusion.

Particle Tracking Summary

Massless tracer particles were released at (0, 0) and numerically transported to position **x** at time *t* by:

$$\mathbf{x}_{t+\Delta t}=\mathbf{x}_t+u_t\Delta t+\mathbf{Z}\sqrt{2D\Delta t}$$

where *u* is the velocity field, **Z** is comprised of random numbers with mean 0 and variance 1, and *D* is diffusivity, set here to 1.5x10^{-5} m^2/s.

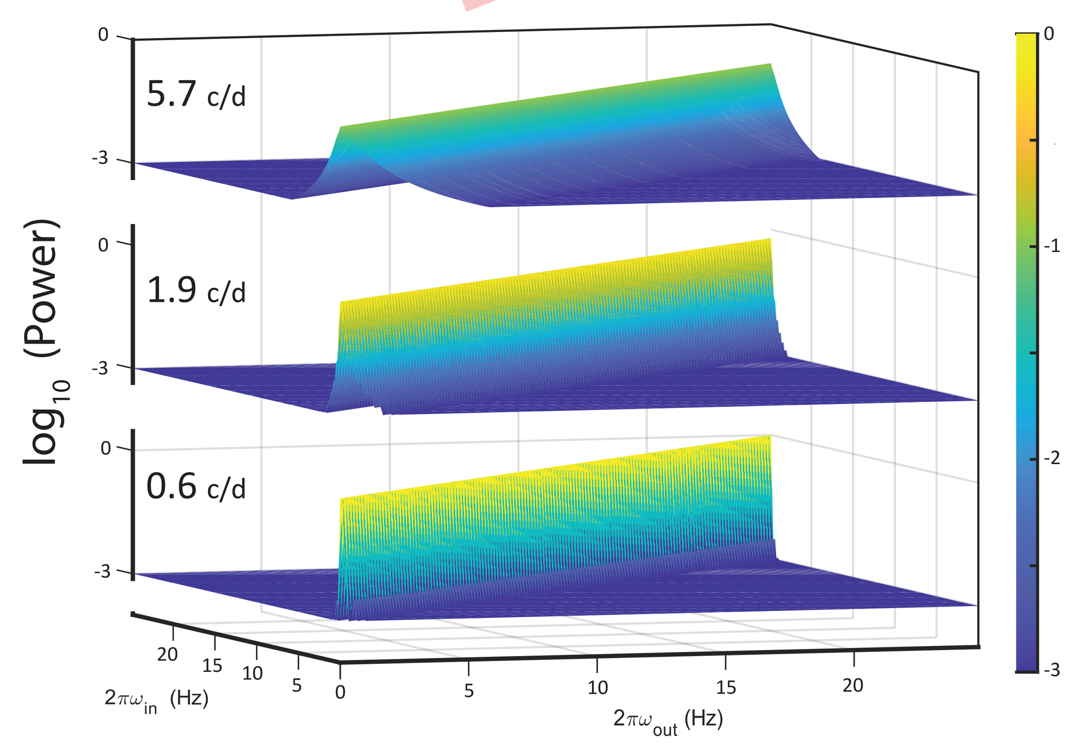
The velocity field was generated via a 2D finite-element model with interacting cylinder wakes to simulate grid turbulence with the below parameters:

- 60 sec simulation time
- Pitch = 2.5 cm
- Cylinder diameters: 1 cm, 1.5 cm
- U_0 = 10 cm/s
- Reynolds No. ≈ 100
- Schmidt No. = 1
- 50 Hz time resolution
- 500 μm spatial grid

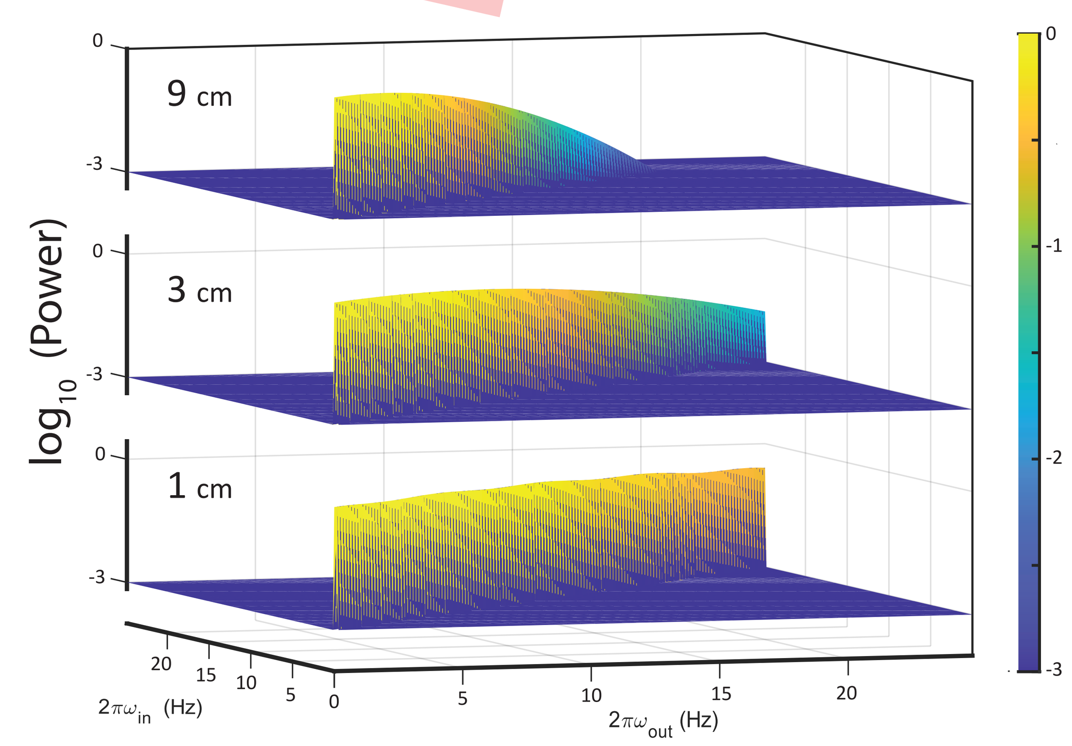
Tootoonian, S., True, A.C., Crimaldi, J.P., Schaefer, A.T. (in review). Quantifying spectral information about source separation in multisource odour plumes.

Turbulent Flow

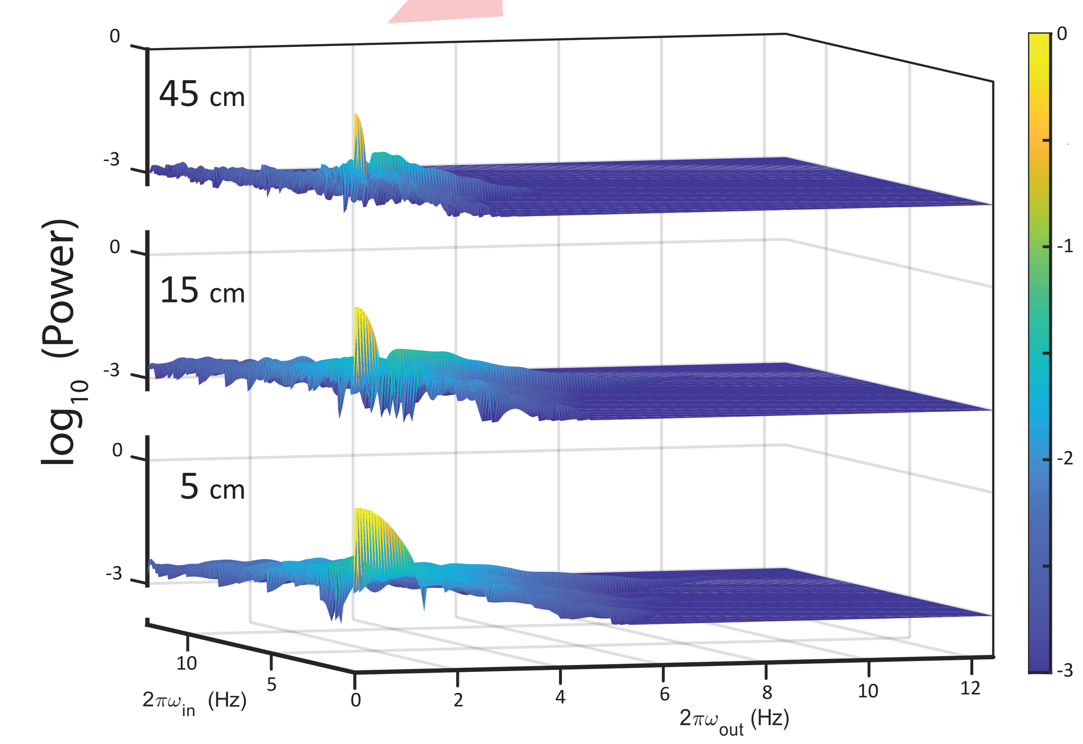
Fluid flow typically mixes these limiting cases. There is a component of frequency spreading similar to active sensation because particles released at nearby times are coupled by the flow. There is also a component of filtering, because particles that are well-separated in time are independent.



Brownian sensor motion (eye movements): Diffusion constant 0.006 deg^2/s. Spatial frequencies: 0.6, 1.9, and 5.7 c/d.



Diffusion with ideal laminar flow: Diffusion constant 0.012 cm^2/s, flow velocity 6 cm/s, sensor distance: 1, 3, and 9 cm.



Computational fluid dynamics simulation of flow as in upper right panel: Sensor distance: 5, 15, and 45 cm.

Conclusions

A common analytical framework can encompass the effects of active sensation and fluid flows on the dynamics of sensory inputs.

Sensor movement and fluid flow transform the frequency content of the source. The spectrum at the sensor has a wider range of frequencies than at the source, reflecting the combined effects of both processes.

Sensor movement convolves the source spectrum with a fixed kernel determined by movement statistics.

Fluid flows have a more complex effect:

- Close to the source, or at low temporal frequencies, the power spectrum at the sensor retains information about the source's spectral content.
- Far from the source, or at high temporal frequencies, the power spectrum at the sensor primarily reflects the dynamics of the flow.