Brain mechanisms of behavior (PSY 445)
Lecture 12

Required reading:
Reading a neural code.

Further readings:
An Optimal Preparation for Studying Optimization.

The animal:
Flies are an incredibly successful Order of insects, and are very useful model systems for many aspects of biology. Genetics would never have progressed so rapidly without Drosophila, the common fruit fly (despite Sarah Palin’s opinion to the contrary… http://www.youtube.com/watch?v=Eg1vleuQT1s). Much of our current understanding of the molecular mechanisms of learning and memory also come from fruit flies. But in Germany in the 1950’s, scientists in the emerging field of cybernetics began to use the blowfly Calliphora as a model system to understand the neural mechanisms of behavior. Cybernetics is the study of control systems, specifically those that have a feedback loop, such as the loop connecting sensation and action. For a simple demonstration of the sensation-action loop, just observe how your visual input changes when you turn your head. While cybernetics can refer to machines or to any system in general, the proponents of biological cybernetics looked to nature to learn how nervous systems had evolved to efficiently and robustly solve very complicated real-world control problems.

Calliphora erythrocephala, the blue blowfly.

The sensation-action loop.
The cyberneticists chose the fly as a model system because they were interested in how sensory feedback from the visual system can be used to control flight. One look at a fly will reveal how strikingly prominent their eyes are, and anybody who has ever tried to catch one knows that they are extremely successful at using visual input to guide their flight behavior.

**The behavior:**
Flies chase other flies. Both females and males will chase each other, although when males chase females as part of their courtship behavior, their pursuit is much longer and much more accurate, demonstrating incredibly fast flight control. They can make course corrections in as fast as 30 ms, which is remarkably fast for a complete sensory-motor action. By comparison, the evoked response in the membrane potential of a vertebrate photoreceptor has not even started in 30 ms! Imagine a fly navigating through a forest at top speed. In order to pursue a female, avoid obstacles, and correct for the effects of the wind and other flight instabilities, the fly must continually estimate its heading direction. How does it do this?

**Optic flow:**
If you’ve ever played around with a flight simulator, you instinctively understand how optic flow produces visual feedback that is critical for course stabilization and flight control. Optic flow is the visual motion stimulus that is produced when you (or an organism) moves through the environment. If you are simply moving straight forward, the optic flow...
Optic flow is generated by self-motion.

What do each of these flow fields convey about heading?

Calliphora.
appears to grow out of a central point ahead of you, and stream past you to the sides. The central origin of the optic flow corresponds to your heading direction. Rigid horizontal motion corresponds to yaw (a plane, or a fly, turning to the right or left). Spiral flow around a central point corresponds to roll. Vertical flow corresponds to pitch. Thus geometric patterns in optic flow can be used to extract roll, pitch, and yaw, the three axes of motion that a pilot needs to use for flight control.

Compensatory response for course stabilization. The drum is rotated back and forth, producing horizontal motion (blue trace). The tethered fly tries to compensate, and the resulting torque produced by the fly can be measured (green trace).
Flight behavior can be studied in the lab. In fact, when a fly is suspended from a wire inside a rotating drum so that the visual scene in front of the fly moves to the right, the fly uses its wings to turn its body to the right, presumably to try to maintain what it perceives as its current heading direction. In other words, the fly reacts to changes in the optic flow to try and stabilize the wide-field visual pattern on its retina, which will stabilize its course. This course-correction behavior is critically dependent on a small set of neurons in the fly visual system, called the *tangential neurons*. These 50 or so identified neurons, in a brain region called the *lobular plate*, respond to wide-field visual motion. There are neurons that respond to each of the kinds of optic flow that a pilot would care about: horizontal motion, vertical motion, spiral motion, expansion and contraction, as well as combinations of these. If these tangential neurons are lesioned, the fly can no longer make course corrections in a rotating drum. This demonstrates that these neurons are necessary for stabilizing heading direction, which is critical for chasing potential mating partners and avoiding obstacles. This suggests that there has probably been strong evolutionary pressure on the performance of these neurons. One of these neurons, H1, is particularly accessible experimentally, allowing stable extracellular recordings for hours and even days. H1 responds to rigid wide-field horizontal motion.

In a series of papers over the past decade, de Ruyter van Steveninck, Bialek, and colleagues have exploited the accessibility of H1 and the constraints from fly behavior to address a number of general questions in neural coding and computation. This work combines experiment, theory, and new methods of data analysis to quantify the per-
Usually we present stimuli, and try to make sense of neuronal responses. But the animal faces the opposite task.

**Fig. 1.** Schematic view of the decoding process. The “black box” filters the spike train input \( \{t_i\} \) to produce an estimate \( \hat{s} = f(t) \) of the stimulus.

What information does a spike train convey to the animal? Do spikes represent features or continuous signals? How much information is carried by the spike train? Is the reliability limited by physics of the sensory receptors, or by noise in the brain?
formance of the fly's visual system. Rather than addressing the cellular mechanisms that underlie the neuron's behavior (such as we saw with the circuits underlying crayfish tail-flip or Aplysia gill-withdrawal), their approach has been to address questions about why the neuron acts the way it does. What problem is the fly trying to solve? How good is the system at solving this problem? What aspects of the system's response are essential for this performance? What information does a spike train convey to the animal? Do spikes represent features (like an oriented bar, or the face of Jennifer Aniston), or do they represent continuous signals? How much information is carried by the spike train? Is the reliability limited by the physics of the sensory receptors (external noise) or by the noise in the brain (internal noise, noisy neurons)?

One of the things that makes the Bialek et al. paper so cool is the startling insight in the opening lines. In the traditional approach to trying to understand the brain, we know what the stimulus is (because we presented it), and we try to figure out how the neuron responds. But the organism faces the opposite task — it knows what the neural response is, and from that response it must try to figure out what the stimulus was. This insight inspired Bialek et al. to use an approach called reverse correlation to try to understand what each spike in H1 tells the fly about the visual world. In this approach, they cross-correlated the spike train with the visual stimulus to try to get an estimate of the average stimulus that preceded each spike. What does this mean? One way to try

The reconstruction filter is solved by reverse correlation. It resembles a PSP. Thus a synapse could decode individual spike trains to reconstruct the stimulus.

How good are the reconstructions? As good as possible given photoreceptor noise, which comes from the random arrival of photons. The spiketrain conveys 64 bits/s of information.

![Graph](https://via.placeholder.com/150)

**Fig. 3.** Stimulus level (smooth curve) and spectral density of displacement noise from the reconstruction (middle curve). The bottom curve is the limit to the resolution of small displacements (valid for frequencies >10 Hz) set by noise in the photoreceptor array (5).
to visualize it is to imagine that you’re listening to the spikes from H1. Each time you hear a spike, you take a snapshot of the visual stimulus. Repeat this procedure for 100,000 spikes, and then average together all those snapshots. The resulting “average snapshot” gives you some idea of what in the stimulus was causing H1 to fire. This average snapshot is sometimes called the spike-triggered average, or the reverse correlation kernel. This is what Bialek et al. used for their reconstruction filter. In the next step, they used this filter to try and reconstruct the continuously varying stimulus from the spiketrain. They used a different set of data from the one that they used to estimate the filter. Essentially, they took the “average snapshot,” and pasted down a copy of it for each spike, at the time it occurred. Then they added them all together. The result is a predicted velocity waveform that was surprisingly accurate when compared to the actual stimulus. One reason this worked well is that their stimulus contained only horizontal motion, which is what H1 is sensitive to. Nevertheless, it is amazing that one cell can convey so much information.

The response of H1 to complex, dynamic inputs exhibits some remarkable features. The spike train of H1 actually can be decoded to reconstruct an estimate of a time varying velocity signal. Further, this estimate is so precise that it is almost as accurate as possible, given that the fly looks out at the world through optics with finite resolution and that the signals in the photoreceptor cells of the retina are noisy. This photoreceptor noise in turn comes largely from the random arrival of photons, even at relatively high light levels. On time scales of relevance to fly behavior, the precision of the reconstructions corresponds to motions that are a small fraction of the spacing between receptors on the retina. This “hyperacuity” is confirmed in more direct experiments using the pattern of action potentials from H1 to discriminate between motion steps of different sizes. This is a clear example where the performance of the neuron closely approaches the limits imposed by the physics of the visual inputs.

We can also ask how efficiently the outputs of neural computation are represented in the spike trains. To answer this, it is useful to examine the amount of “information” in the spike train. Information, in this context, is a statistical measure of stimulus-evoked responses that quantifies both the reliability of responses to specific stimuli as well as the richness of the space of stimuli encoded by the neuron. There is a practical method for directly measuring information transmission in spiking neurons that does not require assumptions about which aspects of the stimulus are important to the neuron or which aspects of the neural response are most informative. In this way, direct methods for measuring information can help remove experimenter bias. Using this technique, Bialek et al. found that H1 transmits information at surprisingly high rates, up to 64 bits per second. A bit is just a unit of information (a 1 or a 0), the same unit used to measure how much information is stored in a file, or how fast information is transferred through a cable. The information rate of the H1 spiketrain is within a factor of two of the limit set by the variability (or “entropy”) of the neuron’s responses. Thus the neuron is transmitting nearly as much information as is theoretically possible.

By using the reverse approach, and looking at neural coding from the perspective of the organism reading the neural code rather than the perspective of the experimenter pre-
senting the stimulus, Bialek et al. were able to provide answers to the new kinds of questions they asked. What information does a spike train convey to the animal? Do spikes represent features or continuous signals? The neuron conveys information about the continuous velocity signal. How much information is carried by the spike train? 64 bits per second! Is the reliability limited by the physics of the sensory receptors or by noise in the brain? The system transmits information very close to the theoretical limits imposed by the laws of physics.