Sensory-Motor Resonance and the Genesis of Search Behavior in Flies

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Most complex behavior results not from a simple feed forward expression of centrally patterned motor code, but rather it emerges from a closed-loop interaction among an animal's brain, its musculo-skeletal system, and the physical environment. Our laboratory uses the fruit fly, *Drosophila melanogaster*, as a model system for studying how brain, body, and world interact to produce the behavior. Ultimately, we wish to construct a model that can explain all the spatial and temporal nuances in an animal's flight behavior – why and where it takes off, ascends, turns, and lands.

Although the flight of a fly appears random and chaotic, it is a highly structured behavior. Flies explore their environment using a series of straight sequences interspersed with rapid turns called saccades - named in analogy with the rapid rotations of our eyes - during which the animal changes its flight heading by 90^o in 50 ms. Superficially, the flight trajectory resembles a random walk. However, both the timing and direction of each saccade are determined by visual feedback. In order to determine what features of optic flow serve to trigger each saccade, we have reconstructed what a fly sees as at explores a structured flight arena. This is accomplished by tracking the fly's motion in 3D, and calculating both the pattern of optic flow it would experience, and the resulting output of a 2D array of Hassenstein-Reichardt elementary motion detectors (EMDs), modeled after prior behavior and physiological measurements in flies. The basic approach is to calculate reverse correlation of the optic flow and EMD activity patterns prior to each saccade. This technique is common in studies of spike coding in sensory neurons. Here, we use rapid behavioral events, the saccades, in place of spikes as the alignment points to construct a signal average of the sensory stimulus. The resulting average represents the spatio-temporal pattern of flow most likely to elicit a saccade within the parameter space determined by the visual landscape and the animal's flight kinematics. The patterns emerging from this analysis suggest that each saccade is triggered by a sharp discontinuity in horizontal optic flow, such that the fly experiences front-to-back motion on one side, and no motion on the other. The bilateral imbalance of the pattern determines the direction of the subsequent saccade. If the strong front-to-back motion occurs on the left side, the animal saccades to the right and vice versa. In this way, the saccade trigger appears to represent a collision avoidance reflex, as the reflex functions to move the animal away from looming objects. Curiously, this simple behavior cannot be explained by classic models of flight control based on optomotor equilibrium. In such models, the animal should turn *towards* the front-to-back flow, not away from it.

The simplest neural model that could explain the results is one consisting of two large field cells acting as spatio-temporal filters. These putative cells would function to integrate the pattern of optic flow until reaching a threshold and triggering a saccade. The spatial filtering properties of such cells might bear some resemblance to the reverse correlation functions described above. To test this idea further, we developed a virtual reality version of the free flight experiments, in which we record the kinematic responses of tethered flies presented with flow fields created in a cylindrical LED display. The results of these experiments suggest that the collision avoidance system is composed of two bilateral expansion detector systems, centered 90^o to the left and right. The animal possess an additional expansion detector centered frontally that activates, not collision avoidance, but rather the stereotyped landing response. Thus, the direction of each turn and the choice of whether to turn or land are determined by the position of a the focus of expansion that the fly experiences as it moves through its visual environment.

These experiments shed light on only a small fraction of the fly's impressive flight behavior. Nevertheless, the analysis suggests how quite complicated patterns of motion might emerge from a rather simple set of sensory-motor reflexes, when placed within a larger control loop that includes the animal's motion and the resulting changes in afferent feedback. In more recent experiments, we are trying to determine how sensory information from other modalities, especially the olfactory system, can bias the visual control loop and lead an individual towards food, shelter, and mates.