Giant Neuron Input in Mutant and Wild Type *Drosophila*

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Summary. Giant neurons of wild type *Drosophila* can be driven to spike by various mechanical inputs, but not by visual inputs. In two genetically and phenotypically different mutants visual input can drive the giant neurons. This is taken as evidence that such a connection may also exist in wild type *Drosophila*, at subthreshold level.

2. In at least one of the mutant stocks the giant neuron provides inputs to all contralateral dorsal longitudinal muscle fibers.

3. In mutant animals, visual input elicits spike activity in the giant neuron and flight.

4. Visual input to mutant giant neurons is mediated by the compound eyes, not the ocelli. Each neuron receives binocular activation.

5. The giant neuron responds to the onset, but not the end, of a flash of light.

6. An analysis of tarsal and wind receptor input to the giant neuron was carried out. Tarsal inputs are an important conjugate to wind input for eliciting giant neuron activity. The interaction of these inputs was further corroborated by showing that either can influence the latency and probability of the response of the giant neuron to the other.

7. The giant neuron in *Drosophila* and the DMD neurons of the locust are compared. Results indicate that the previously described anatomical analogy between these two systems can be extended in two ways: to a physiological input (vision), and to the behavioral function of the output (jumping).

Introduction

The bilateral pair of giant motorneurons in *Drosophila* was first described by Power (1948). The giant neuron is the largest cell in the drosophilian nervous system. Its axon measures approximately 4 to 8 μm in diameter over a length of more than 200 μm. Although Power was unable to locate its cell body, he found that the giant axon extends caudally from the brain to innervate the ipsilateral tergal depressor of the trochanter (TDT) muscle. The TDT muscles are a bilateral pair of large tubular fast muscles which could function as wing elevators or mesothoracic leg extensor (jump) muscles (Pringle, 1968). Power noted that in the mesothoracic nervous system the giant neuron has a branch which decussates with the branch of the contralateral homologue and exits through the contralateral dorsal mesothoracic root to innervate all fibers of the contralateral dorsal longitudinal muscle (DLM) (Power, 1948).
Because the power for wing movement in flies is produced by fibrillar muscles, the timing of contraction of the power flight muscles is determined by stretching of the thorax instead of by the time of arrival of motor-neuron action potentials at the nerve muscle junction. The thorax resonates during flight alternately stretching the wing elevator muscles (dorsal ventral muscles, DVMs), and the wing depressor muscles (dorsal longitudinal muscles, DLMs), thus causing them to contract. Such a system, however, needs an additional mechanism to start the oscillations of the thorax. The giant neuron-tergal depressor of the trochanter complex could act as a fast-reflex starter of flight because the TDT muscle is innervated by the giant neuron (Power, 1948; Levine and Tracey, 1973). The TDT muscle can therefore provide both power to the legs for jumping, and the necessary twitch to start the thoracic oscillations.

Levine and Tracey (1973) have confirmed the continuity of the giant neuron in the cervical connective with its process in the dorsal mesothoracic nerve by filling the axons (Iles and Mulloney, 1971) with cobalt sulphide. This strengthened Power's conclusion that the giant is a TDT motorneuron. Levine and Tracey also showed that the giant neuron supplies input to the DLM fibers, and that the giant neuron is presynaptic to a DVM motorneuron. When the giant neuron fires, this connectivity leads to a stereotyped motor output pattern which has been referred to as the triadic motor output pattern or triad (Levine and Tracey, 1973). The giant firing is characterized by a spike in the TDT muscle which follows the activation of the giant neuron with a short and constant latency. One or two tenths of a millisecond after the onset of the TDT spike, spikes occur in all the DLM fibers. Finally, followed by a much longer and more variable delay (2 to 8 msec) spikes occur in all the DVM fibers. This temporal pattern is the triad. Levine and Tracey further characterized the triad by the frequencies at which the different components (TDT, DLM, and DVM) of the output ceased one-to-one following of the electrical stimulation of the giant neuron. The DVM fibers drop at between 0.2 and 2.0 Hz. The remaining dyad of TDT and DLM follows electrical stimuli up to 30 to 60 Hz.

The probable behavioral significance of the connections of the giant neuron to the DLM, DVM, and TDT muscle lies in the fibrillar nature of the DLMs and DVMs. The contraction of the non-fibrillar—twitch—TDT muscle, elicited by the firing of the giant neuron, will start thoracic oscillations. Because the DLMs and DVMs have also been activated by the giant neuron, thoracic oscillations started by the TDT muscle will elicit contractions in the fibrillar DLMs and DVMs. There are two possible sequences of fiber activity at the start of flight. The giant may fire, causing the fly to jump and activate the indirect, power, flight muscles.