Synchronized Activity in the Insect Brain

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Among the electrical signals that can be recorded from the vertebrate cortex are voltage oscillations in the frequency range 40–70 Hz (γ-waves). For some years the possible role of these waves as information carriers has been under discussion. Relatively high-level functions such as "feature linking" have been proposed for them, and they have even been considered in the context of phenomena such as "awareness" and "consciousness" [1]. The insect brain exhibits high-frequency (hf) oscillations in the range of 100–200 Hz that have much in common with the γ-waves, but their function is interpreted differently.

Under suitable illumination, oscillations in the frequency range from 100 to 200 Hz can be recorded with extracellular electrodes in the optic lobes of Diptera [2] (Fig. 1). They are most commonly observed under large-area illumination, and their amplitude depends on the light intensity and on the state of adaptation of the eye. We have studied these oscillations in the blowfly *Calliphora* under stimulating conditions that facilitate comparison with the γ-waves.

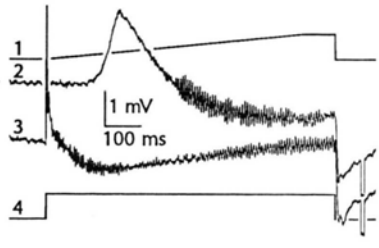

Fig. 1. Traces 1 and 4: Time-courses of stimulus-light intensity; traces 2 and 3: summed potential recorded from an intact *Calliphora* between cornea and posterior head capsule. The hf oscillations are superimposed on the voltage curves typical of the electroretinogram (on-effect and negative sustained potential). These appear not only when the light is turned on suddenly (trace 3) but also when the intensity increases gradually (trace 2).

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The main findings were as follows:

1. The oscillations first arise in the optic lobes. The receptor potentials of the photoreceptors themselves include no specific components in the frequency range of the hf oscillations.

2. The frequency of the hf oscillations at which their amplitude is greatest is largely independent of stimulus parameters.

3. When a stepwise stimulus is applied, the phase of the oscillations is initially synchronized with the stimulus onset, but after some time this synchronization disappears if responses to several stimuli given one after another are compared (Fig. 1, trace 3).

4. Oscillations also appear at a certain level of illumination when the light intensity is increased gradually, rather than abruptly (Fig. 1, trace 2).

5. hf-oscillation is a cooperative phenomenon. When three light sources in a row are turned on simultaneously, the stimulus can elicit large oscillations even though turning on the two outer lights alone, or the middle light alone, does not give rise to hf oscillations at all.

6. The hf oscillations are synchronized over large parts of the brain.

7. In the case of at least one class of neurons, the so-called L neurons of the lamina, it has been shown by intracellular recording that their membrane potential oscillates at about the hf frequency (Fig. 2). This finding implies that numerous L neurons in large parts of the lamina are oscillating synchronously.

The properties of the hf oscillation listed above correspond in many respects to those described for the γ-waves of the vertebrate cortex [3–6]. One

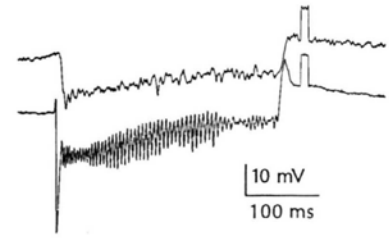

Fig. 2. Intracellular recordings from an L neuron of *Calliphora*. At a relative stimulus intensity I of 10^{-3}, the neuron is hyperpolarized (upper trace). At $I = 10^{0}$ hf oscillations are superimposed on the hyperpolarization (lower trace).

characteristic difference is that the frequency of the hf oscillations in the fly brain is about three times that of the γ-waves.

The arrangement of the L neurons in the fly lamina is retinotopic; that is, they are arrayed in such a way as to form a map of the retina. The L neurons are not divided into spatially distinct subgroups representing various features of objects such as shape, color, movement or orientation. In the lamina, then, there is no problem of "binding" such as arises in the vertebrate cortex, where different features of a single object are represented at *different* sites in the brain. It follows that the function of the hf oscillations cannot be to solve a binding problem. Furthermore, evidence that the hf oscillations have anything to do with phenomena such as "awareness" or "mind" is not expected.

The response of the L neurons in the lamina to a light stimulus consists of hyperpolarization (Fig. 2). Under large-area illumination, the L-neuron hyperpolarization is known to decrease by inhibition a few ms after onset of the response. This delayed negative feedback is tentatively regarded as the cause of the hf oscillations. The mechanism of inhibition is not known. It could well be that large, tangential cells – for example, the serotonergic tangential cells that have been found in the optic lobes of Diptera [7] contribute to this inhibition. The function of the inhibition is presumably to adjust the working range and/or the sensitivity of the L neurons in the lamina – and, perhaps, to affect similarly the neurons in other optic ganglia [8].

The inhibition of the L neurons increases with increasing light intensity and size of the stimulated retinal area. The weak inhibition associated with small, low-intensity stimuli is *not* accompanied by oscillations, but after these parameters have become large enough, oscillations develop. The functional significance of the hf oscillations could be to open rapidly inactivating channels at high frequency, thereby enabling particularly effective inhibition in case of strong stimuli. The many analogous characteristics of the hf oscillations and the γ-waves suggest that the γ-waves could function similarly. The higher frequency of the hf waves could perhaps be related to the shorter conduction times of signals in the fly brain.

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