Tonic Transmitter Release in a Graded Potential Synapse

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SUMMARY AND CONCLUSIONS

1. We studied graded synaptic transmission in the fly photoreceptor-interneuron synapse by using intracellular in situ recordings from pre- and postsynaptic cells.

2. A large presynaptic hyperpolarization after light adaptation, caused by the activation of the electrogenic Na+/K+ pump, drastically reduced the conspicuous postsynaptic dark noise. At the same time, the postsynaptic neurons depolarized, with an increase of input resistance of 5–10 MΩ.

3. The spectral characteristics of the postsynaptic membrane noise in dark and during noise reduction, together with the other results, suggested that the transmitter release decreased dramatically ~12 mV below the resting potential of the presynaptic photoreceptors.

4. During the postsynaptic noise reduction, the saturated and subsaturated first-order visual interneuron responses were increased up to 9 mV with a time constant of recovery of ~10 s. This increase was shown to be caused by the negative shift of the reversal potential of the transmitter-gated (mainly Cl-) conductance, caused apparently by the reduced transmitter input.

5. The results strongly suggest that the presynaptic transmitter release in fly is tonic, even in dark, and further support the modulation of the synaptic voltage transfer by postsynaptic Cl-extrusion.

RESULTS

The results in this paper are based on recordings from 20 LMCs and 20 photoreceptors. First we studied the changes in the pre- and postsynaptic RP after light adaptation. Intense light stimulation induced a large hyperpolarizing afterpotential in photoreceptors (Fig. 1A), which was due to the increased activity of the electrogenic Na+/K+ pump, as reported earlier (Hamdorf et al. 1988; Jansonius 1990). Intracellular recordings from presynaptic photoreceptors showed clear dependence of this afterpotential on the duration of the adapting light stimulus (Fig. 2C). During the presynaptic pump potential the postsynaptic neurons depolarized by 2–6 mV and the conspicuous postsynaptic noise was drastically reduced (Figs. 1A and 2B). In this same period the IR of the LMCs increased by 7.4 ± 2.9 (SD) MΩ (n = 5). These findings suggest that the tonic (dark) transmitter release from the photoreceptors was strongly reduced during the presynaptic pump potential. The power spectrum of the dark noise in postsynaptic LMCs normally consists of two clearly distinguishable components (Laughlin et al. 1987). The low-frequency component of the spectrum was attenuated considerably during the presynaptic pump potential, i.e., during the noiseless and depolarized period of the postsynaptic LMCs (Fig. 1B). This further supports the hypothesis of the tonic transmitter release.

The conspicuous postsynaptic noise reappeared at the time when the presynaptic hyperpolarization recovered to the
voltage of 12 ± 1 mV (n = 15, both for photoreceptors and LMCs) from the RP (Fig. 1A). This implies that the transmitter release has a strong dependence on the presynaptic membrane potential such that the transmitter release is much reduced below about −73 mV, when normally the dark RP in photoreceptors was −61 ± 7 mV (n = 20).

The properties of synaptic voltage transfer were studied by applying test flashes of varying intensity before and during the presynaptic pump potential. Under this period the postsynaptic responses increased in amplitude up to 9 ± 0.2 mV (n = 15). This increase was largest with a 2-s adapting light stimulus and with test flashes that saturated the postsynaptic LMC voltage (Fig. 2). The increase of the amplitude of the LMC responses depended directly on the presynaptic pump potential (Fig. 2C). With adapting pulses >2 s, the depolarizing after-potential (PDA and/or non-PDA) in presynaptic
The negative shift of the E_{rev} was 29 ± 3 mV limited by the increased response lasting was not possible. Because the perfect current clamping of the OR during the LMC reversal potential was indeed hyperpolarized during continuous even in dark. In this sense the synapse is similar before the presynaptic hyperpolarization (as in Fig. 3). This is most probably brought about by the action of the tonic Cl⁻ extrusion mechanism (Uusitalo and Weckström 1994) in the absence of a tonic-transmitter-mediated Cl⁻ influx, causing a reduction in intracellular [Cl⁻]. Although the increase of the postsynaptic response amplitude is caused by relatively unphysiological stimulation, it is an indicator of the underlying synaptic adaptation mechanisms. The manipulation of the synaptic transmitter release in the manner described in the present work could be an important tool in further investigations of this graded synaptic transmission. The shifts in Cl⁻ reversal potential described in this work and previously (Uusitalo and Weckström 1994) suggest a possible way for the gain regulation in the synapse.

The continuous transmitter release in the photoreceptor-LMC synapse is likely to be an adaptation to increase gain and sensitivity of the visual system. Having a tonic, as opposed to pulsed, transmitter release mechanism allows the photoreceptors to transmit signals of both polarity, i.e., responses to both positive and negative contrasts with high gain (Howard et al. 1987; Juusola et al. 1994, 1995; Laughlin et al. 1987). The dipteran photoreceptor-LMC synapse has been called a high-gain synapse (Laughlin et al. 1987). This property is partially invested in the properties of the postsynaptic histamine-gated Cl⁻ channels, which appear to have a high cooperativity (Hardie 1989) and, accordingly, a steep dependence of their open probability from the transmitter concentration. However, the continuous transmitter release is equally important as a mechanism that forces the synaptic voltage transfer to operate near the steepest part of the governing function, regardless of the postsynaptic DC voltage (Laughlin et al. 1987), which is in turn largely defined by the adapting intensity of the ambient light.

We thank A. French and R. Hardie for critical comments on this work. S. Leo and A. Vanhala for technical support.

This work was supported by the Oskar Öflund Foundation (R. O. Uusitalo), Finnish Eye Foundation (R. O. Uusitalo), the Finnish Medical Foundation Duodecim (R. O. Uusitalo and M. Juusola), and by the Academy of Finland.

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Received 18 November 1994; accepted in final form 3 April 1995.

REFERENCES


TONIC TRANSMITTER RELEASE


