

## SHORT COMMUNICATION

### PLATEAU POTENTIALS IN AN INSECT MOTONEURONE CAN BE DRIVEN BY SYNAPTIC STIMULATION

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Cyclical patterns of behaviour such as respiration and locomotion are generated by groups of neurones whose output depends not only upon their synaptic interconnections but also on the intrinsic membrane properties of individual cells. For example, the ionic conductances of some neurones in rhythm-generating circuits allow these cells to respond to non-patterned excitatory synaptic drive with 'plateau' or 'driver' potentials: prolonged, regenerative depolarizations which can drive bursts of impulses and, thereby, contribute to characteristics of the motor rhythm (Russell and Hartline, 1978, 1982; Tazaki and Cooke, 1979*a–c*, 1983*a–c*, 1986, 1990). Plateau potentials are not restricted to interneurons of the central pattern generator; they may also be recorded from motoneurons, which form the final output to muscles. Thus, plateau potentials have been recorded from locomotor motoneurons from the crayfish (Sillar and Elson, 1986), lamprey (Wallén and Grillner, 1987), cat (Hounsgaard *et al.* 1988) and turtle (Hounsgaard and Kiehn, 1989) (see also review by Kiehn, 1991).

Although the consensus had been that insect neurones cannot generate plateau potentials, recent studies have demonstrated that some leg motoneurons of the cockroach (*Periplaneta americana*) (Hancox and Pitman, 1991) and flight interneurons of the locust (*Locusta migratoria*) (Ramirez and Pearson, 1991*a,b*) can actually generate plateau potentials. It has been shown that plateau potentials in locust flight interneurons can be driven by synaptic input (Ramirez and Pearson, 1991*a,b*), but those recorded from cockroach leg motoneurons were evoked by current injected into the neurone soma (Hancox and Pitman, 1991). We report here that plateau potentials can be elicited by presynaptic stimulation of the 'fast' coxal depressor motoneurone ( $D_f$ ) of the cockroach (*Periplaneta americana*). This important observation indicates that the plateau potentials recorded from this preparation could, indeed, play a significant role in shaping motor output.

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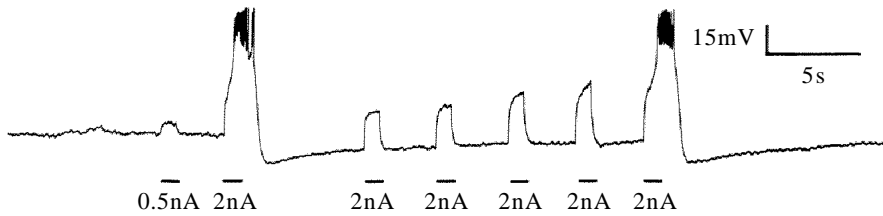


Fig. 1. Plateau potentials in motoneurone  $D_f$  are followed by a prolonged after-hyperpolarization, during which the threshold for plateau potentials is elevated; initially a 2 nA current pulse (current pulses indicated by horizontal bars) was sufficient to evoke a plateau potential, but similar pulses remained subthreshold for nearly 20 s after a plateau. Resting potential  $-74$  mV.

Because the major presynaptic inputs to  $D_f$  have not been identified, electrical stimuli were applied to connectives or peripheral nerves. Recordings were taken from the soma of  $D_f$  in an isolated ganglia preparation (Pitman, 1979) under two-electrode current-clamp; a length of the peripheral nerve 5 (N5) contralateral to the impaled soma was left attached to the metathoracic ganglion to allow extracellular stimulation with a suction electrode. (Intracellular dye-injection has established that motoneurone  $D_f$  does not send processes into the contralateral nerve 5; Pitman *et al.* 1972.)

Plateau potentials could be elicited in  $D_f$  by relatively long-duration, suprathreshold current pulses applied to the soma; when shorter pulses were applied, plateau potentials could outlast the applied pulse (Fig. 1). These events were characterised by an inflection on the rising phase and a plateau phase that was often surmounted by attenuated axonal action potentials. Plateaux were also followed by a relatively prolonged after-hyperpolarization (AHP) during which the neurone was relatively refractory to a previously suprathreshold depolarization (Fig. 1). Following a plateau potential, the neuronal membrane potential took between seconds and tens of seconds to repolarize to the original level. Thus, for depolarizing stimuli of a given strength, the frequency of plateau potential generation was limited by the AHP.

Extracellular stimuli applied to the contralateral nerve 5 caused postsynaptic potentials which, in each of four cells examined, were excitatory. These excitatory postsynaptic potentials (EPSPs) summated during stimulus trains (Fig. 2A), but were unable to generate a depolarization of sufficient magnitude to take the membrane potential of the neurone from its resting value to the threshold for a plateau potential. However, plateau potentials could be evoked by repetitive extracellular stimulation of nerve 5 if the motoneurone was depolarized by sustained intrasomatic current which was, in itself, subthreshold for plateau potential generation (Fig. 2B). Thus, cells under a depolarizing bias could generate plateau potentials in response to synaptic stimulation. Plateau potentials could also be elicited by stimuli applied to the peripheral nerve when the soma was depolarized by subthreshold depolarizing pulses rather than sustained current.

The results presented here show the important point that plateau potentials are accessible to, and can be driven by, synaptic inputs to motoneurone  $D_f$ . These observations are similar to those made upon plateau potentials in crayfish (Sillar and

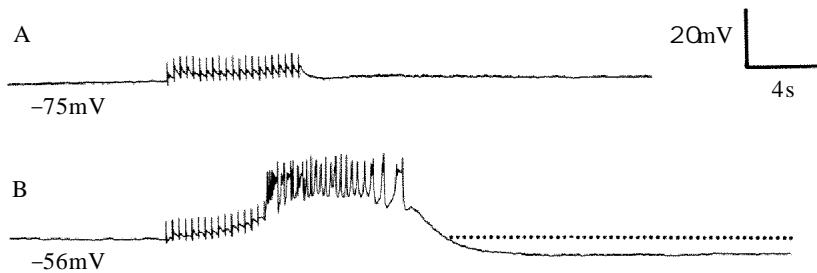


Fig. 2. Synaptic potentials elicited in motoneurone  $D_f$  by electrical stimulation of nerve 5 contralateral to the neurone soma. Although repetitive electrical stimulation fails to evoke a plateau potential at the resting potential ( $-75\text{mV}$ ) (A), depolarizing the membrane potential to  $-56\text{mV}$  enables an identical train of electrical stimuli to elicit a plateau potential (B). The dotted line marks the extent of the after-hyperpolarization that follows the plateau potential.

Elson, 1986) and cat (Crone *et al.* 1988) motoneurones, which can be driven by peripheral afferent inputs. Our observations suggest that plateau potentials may modulate the efficacy of synaptic inputs to the motoneurone: plateau potentials themselves amplify synaptic drive, while the period of refractoriness following each plateau potential limits the effects of presynaptic input.

That EPSPs alone were insufficient to elicit plateau potentials in motoneurone  $D_f$  without a depolarizing bias is perhaps not surprising; recordings were made from an isolated nerve cord preparation in which tonic synaptic drive from the cerebral ganglia and from sensory receptors was absent. As a consequence, the resting potential of  $D_f$  probably would be significantly more negative than in the intact animal.

Our observations indicate, therefore, that plateau potentials may be elicited in the 'fast' coxal depressor motoneurone of the cockroach by excitatory synaptic drive, enabling this neurone to exert a major influence on motor output.

### References

- CRONE, C., HULTBORN, H., KIEHN, O., MAZIERES, L. AND WIGSTRÖM, H. (1988). Maintained changes in motoneuronal excitability by short-lasting synaptic inputs in the decerebrate cat. *J. Physiol., Lond.* **405**, 321–343.
- HANCOX, J. C. AND PITMAN, R. M. (1991). Plateau potentials drive axonal impulse burst in insect motoneurons. *Proc. R. Soc. Lond. B* **244**, 33–38.
- HOUNSGAARD, J., HULTBORN, H., JESPERSEN, B. AND KIEHN, O. (1988). Bistability of  $\alpha$ -motoneurons in the decerebrate cat and the acute spinal cat after intravenous 5-hydroxytryptophan. *J. Physiol., Lond.* **405**, 345–367.
- HOUNSGAARD, J. AND KIEHN, O. (1989). Serotonin induced bistability of turtle motoneurons caused by a nifedipine-sensitive calcium plateau potential. *J. Physiol., Lond.* **414**, 265–282.
- KIEHN, O. (1991). Plateau potentials and active integration in the 'final common pathway' for motor behaviour. *Trends Neurosci.* **14**, 68–73.
- PITMAN, R. M. (1979). Intracellular citrate or externally applied tetraethylammonium ions produce calcium dependent action potentials in an insect motoneurone cell body. *J. Physiol., Lond.* **247**, 511–520.
- PITMAN, R. M., TWEEDLE, C. D. AND COHEN, M. J. (1972). Branching of central neurons: intracellular cobalt injection for light and electron microscopy. *Science* **176**, 412–414.

- RAMIREZ, J. M. AND PEARSON, K. G. (1991a). Octopamine induces bursting and plateau potentials in insect neurones. *Brain Res.* **549**, 332–337.
- RAMIREZ, J. M. AND PEARSON, K. G. (1991b). Octopaminergic modulation of interneurons in the flight system of the locust. *J. Neurophysiol.* **66**, 1522–1537.
- RUSSELL, D. F. AND HARTLINE, D. K. (1978). Bursting neural networks: a reexamination. *Science* **200**, 453–456.
- RUSSELL, D. F. AND HARTLINE, D. K. (1982). Slow active potentials and bursting motor patterns in pyloric network of the lobster, *Panulirus interruptus*. *J. Neurophysiol.* **48**, 914–937.
- SILLAR, K. T. AND ELSON, R. C. (1986). Slow active potentials in walking-leg motor neurones triggered by non-spiking proprioceptive afferents in the crayfish. *J. exp. Biol.* **126**, 445–452.
- TAZAKI, K. AND COOKE, I. M. (1979a). Spontaneous electrical activity and interaction of large and small cells in the cardiac ganglion of the crab *Portunus sanguinolentus*. *J. Neurophysiol.* **42**, 975–999.
- TAZAKI, K. AND COOKE, I. M. (1979b). Isolation and characterization of slow, depolarizing responses of cardiac ganglion neurons in the crab, *Portunus sanguinolentus*. *J. Neurophysiol.* **42**, 1000–1021.
- TAZAKI, K. AND COOKE, I. M. (1979c). The ionic bases of slow, depolarizing response of cardiac ganglion neurons in the crab, *Portunus sanguinolentus*. *J. Neurophysiol.* **42**, 1022–1047.
- TAZAKI, K. AND COOKE, I. M. (1983a). Topographical localization of function in the cardiac ganglion of the crab, *Portunus sanguinolentus*. *J. comp. Physiol. A* **151**, 311–328.
- TAZAKI, K. AND COOKE, I. M. (1983b). Separation of neuronal sites of driver potential and impulse generation by ligaturing in the cardiac ganglion of the lobster, *Homarus americanus*. *J. comp. Physiol. A* **151**, 329–346.
- TAZAKI, K. AND COOKE, I. M. (1983c). Neuronal mechanisms underlying rhythmic bursts in crustacean cardiac ganglia. *Soc. exp. Biol. Symp.* **37**, 129–157.
- TAZAKI, K. AND COOKE, I. M. (1986). Currents under voltage-clamp of burst-forming neurons of the cardiac ganglion of the lobster (*Homarus americanus*). *J. Neurophysiol.* **56**, 1739–1762.
- TAZAKI, K. AND COOKE, I. M. (1990). Characterization of Ca current underlying burst formation in lobster cardiac ganglion motoneurons. *J. Neurophysiol.* **63**, 370–384.
- WALLÉN, P. AND GRILLNER, S. (1987). N-Methyl-D-aspartate receptor induced, inherent oscillatory activity in neurons active during fictive locomotion in the lamprey. *J. Neurosci.* **7**, 2745–2755.