oviducal gland secretions. The control mechanism for this could be analogous to that in the Cecropia silkworm *Hyalophora* where there is a low-temperature requirement (6°–15° C) before neurosecretory cells will initiate the termination of pupal diapause[5].

At present little is known about endogenous control systems in Cirripedia. My observations indicate a possible control mechanism for breeding in *B. balanoides* which would bring cirripedes into line with the general pattern of endocrine control in Arthropods and provide a basis for further experiments.

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Monosynaptic Stochastic Stimulation of Spinal Motoneurones in the Cat

THE artificial nature of a synchronous afferent volley was pointed out many years ago[1] and, although neurophysiological knowledge has been considerably advanced by use of the synchronous volley technique, it has definite limitations in providing a full understanding of reflex mechanisms in the intact animal. Each annulo-spinal ending in a muscle under tension discharges in a quasi-periodic manner, and the differing stretch thresholds in these receptors[2] cause the average discharge frequency of each ending to differ. The timing of the initiation of impulses in one ending will be statistically independent of the times of occurrence of impulses in other endings. The convergence of these asynchronous impulse patterns onto a particular motoneurone represents a situation very different from that of synchronous stimulation and introduces the effects of temporal summation. If the object of the experiment is to establish relationships between afferent and reflex impulse patterns, natural stimulation by stretching muscle has severe limitations, because the temporal impulse patterns arriving at a particular motoneurone cannot be obtained. In the experiments described here, an attempt has been made to overcome this problem while retaining a stimulus which is physiologically realistic.

All experiments were performed on cats which had been made spinal under ether anaesthesia. Many branches of posterior biceps-semitendinosus or gastrocnemius-soleus muscle groups were prepared for stimulation by fine dissection down into the muscle. A motoneurone responding monosynaptically to synchronous stimuli on either of these nerve groups was isolated by way of a ventral root filament. Only afferent branches which caused a detectable depolarization of the motoneurone were used in the experiment. These branches were found by the presence of a reflex spike when the depolarization caused by stimulation of the branch under study was added to a slightly subthreshold depolarization produced by synchronous stimulation of other effective branches. Each useful afferent branch was then separately stimulated by either a periodic or random pulse process such that the stimulus processes for each nerve branch were asynchronous. Stimulus strengths were usually much less than maximum GpI and were adjusted to ensure that at least two separate afferent fibre groups required simultaneous stimulation to produce sufficient summation to evoke a reflex discharge. Stimulus frequencies were varied between 10/sec and 200/sec. The individual stimulus frequencies were adjusted to be within ± 10 per cent of a nominal stimulus frequency.

The nature of asynchronous or stochastic stimulation is illustrated in the pen recordings in Fig. 1. These were obtained by replaying tape recorded stimulus processes and ventral root discharge at a reduced speed and combining two stimulus trains onto a single pen, using polarity to distinguish between them. Fig. 1*A* shows the effect of applying four trains of periodic stimuli, of slightly different frequency, and randomly phased to four afferent nerve groups of the cell the discharge of which is being recorded. In the experiment recorded in Fig. 1*B*, the same cell was subjected to stimulus processes of random or Poisson type with the same average stimulus rate and which were delivered at the same stimulus intensity as in the previous case. In both cases, temporal and spatial summation combine to discharge the cell, and the discharge is noticeably regular in its interspike interval duration. A slowly discharging cell does not have the same regularity.

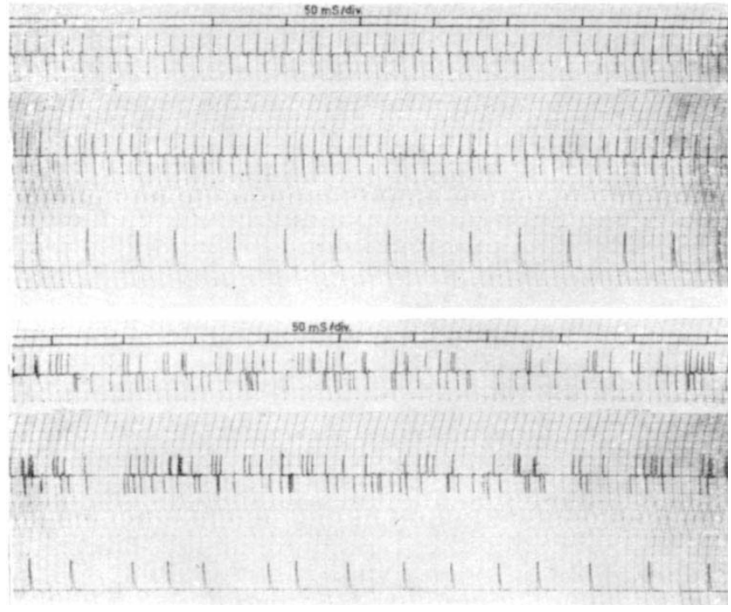

Fig. 1. *A*, Pen recording showing four asynchronous trains of periodic stimuli, each at a nominal frequency of 100/sec, and the simultaneous discharge in a ventral root filament. Individual stimulus strengths were confined to less than max. GpI, and adjusted such that simultaneous stimuli processes on at least three separate pathways were necessary for the cell to discharge. Stimulus impulse deletions indicate where two combined stimulus impulse trains drift into phase. *B*, Four independent Poisson or random stimulus impulse trains, with mean impulse rates approximately 100/sec, applied in place of the four periodic processes in *A*. All other stimulus and recording conditions are identical to those in *A*.

The long term discharge response of motoneurones stimulated with a suddenly applied and maintained stochastic stimulus shows considerable variation. Recordings from the same motoneurone pool with constant stimulus conditions provide discharges which vary from extremely phasic to extremely tonic in nature, with all intermediate combinations of these discharge characteristics. These results suggested a continuous distribution between tonic and phasic properties within a functional motoneurone pool, as other investigators[3,4] have recently suggested, rather than a distinct division into tonic and phasic motoneurones[5].

Motoneurones which discharge tonically were stimulated with a range of frequencies and the stimulus strengths were kept constant on all stimulated pathways. At least 60 sec of continuous recording was made at each stimulus frequency and the mean discharge frequency was calculated from the entire record. The relationship is shown in Fig. 2, where a curve has been drawn for periodic asynchronous stimulation and points are shown for the Poisson pulse rates which were available. This and other similar results indicate an approximately exponential relationship between the mean afferent and efferent frequencies in the afferent range of 30–120/sec (an important physiological range). Frequency limiting usually occurs at an efferent frequency of 10–15 impulses/sec and the afferent frequency at which this discharge rate occurs depends on the individual stimulus intensities. When threshold is exceeded by three, but not two, afferent groups which have been simultaneously stimulated, the stimulus frequency is usually in the range of 100–120 pulses/sec. This frequency limiting has been a consistent finding with various electrical stimulation methods involving GpI fibres only[6,7]. Frequency limiting has previously been ascribed to the effects of recurrent inhibition[8]. In this experimental arrangement, the motoneurones of the excited pool will excite Renshaw cells asynchronously and recurrent inhibition will be operative. Recent experiments measuring frequency transfer characteristics before and after the infusion of dihydro-beta-erythroidine (hydrobromide) indicate that recurrent inhibition does not change the frequency at which limiting occurs. We believe that repolarizing current during "after hyperpolarization" and the depolarization limitations of the Ia afferent pathways are the principal factors in limiting the discharge frequency.

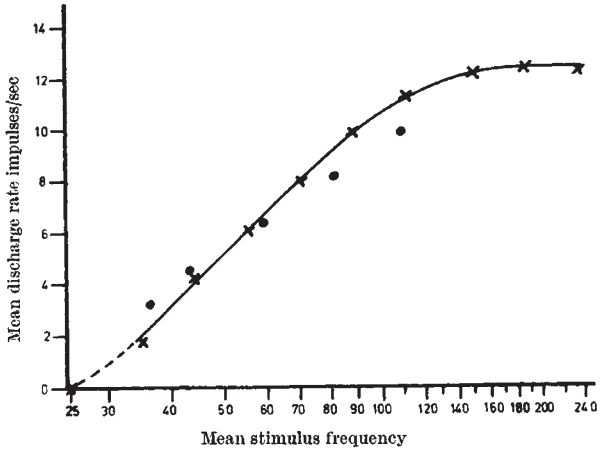

Fig. 2. Results taken from a unit responding tonically to stimulation of gastrocnemius–soleus nerves. All branches of medial and lateral gastrocnemius and soleus muscle groups were arranged on four separate stimulators. The stimulus strength on each was adjusted such that, at a nominal frequency of 100/sec for each stimulator, all but two combinations of pairs were effective in discharging the cell when asynchronous stimulation was applied from two stimulators at a time. Measurements were taken in order of increasing frequency, with a 3 min period without a stimulus between each record. No discharge was obtained at a mean stimulus frequency of 25/sec, which was the next available frequency below 35/sec. The discharge could have ceased at an intermediate frequency. There was no alteration in stimulus strength when Poisson stimuli were used. ×, Asynchronous periodic stimulation; ●, Poisson stimulation.

The frequency transfer curve specifies the stationary transfer properties of a single monosynaptic reflex pathway with a fixed number of stimulated afferent fibres. A more complete description of the reflex pathway would be a family of frequency transfer curves with "recruitment" as a parameter.

The technique of stochastic stimulation offers a method of establishing reflex discharges from neurones excited by means of converging peripheral pathways in a controlled and approximately physiological manner. Modulation in the excitability of the neurone may then be quantitatively measured by changes in the discharge frequency of that cell. A precise knowledge of the afferent temporal patterns is also helpful in investigating input–output relationships.

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Strychnine Block of Neural and Drug-induced Inhibition in the Cerebral Cortex

There have been conflicting reports about the actions of strychnine on cortical inhibitions. Inhibition of cortical neurones by direct cortical stimulation is resistant to strychnine[1,2]. The "recurrent" inhibition of cortical neurones during stimulation of the pyramidal tract has been said to be both resistant to strychnine[1,3] and antagonized by strychnine[4–7].

This investigation of the actions of strychnine on neural and drug-induced inhibitions in the cerebral cortex was started when we realized that strychnine antagonized the depressant actions of noradrenaline and 5-hydroxytryptamine (5-HT) on neurones in the left precruciate cortex.

All experiments were performed on cats anaesthetized with nitrous oxide and methoxyflurane ('Penthrane', Abbott). Drugs were applied iontophoretically from five barrelled micropipettes, the central barrel of which was used for recording the extra cellular spike potentials of cortical neurones. A Hewlett–Packard electronic counter coupled to an ink-recorder was used to analyse the discharges of cortical neurones which were either spontaneous or evoked by L-glutamate. L-Glutamate pulses of 5–10 sec duration were repeated at regular intervals. Changes in cell excitability were assessed by comparing the spontaneous firing frequencies or those induced by L-glutamate, during and after the application of depressant compounds or during stimulation. The duration of inhibition evoked by direct stimulation was measured as the period of suppression of spontaneous or induced firing. Ipsilateral stimulating electrodes were placed in the lateral hypothalamus (*A*11·5, *L*4, *D*-3), mesencephalic reticular formation (*A*3, *L*3, *D*-1) and on the exposed pyramidal tract. A fine bipolar co-axial electrode was inserted directly into the precruciate cerebral cortex to a depth of 1 mm for cortical stimulation.

Strychnine was applied iontophoretically from a barrel containing 10 mmolar strychnine in a solution of 200 mmolar sodium chloride. When applied by currents of 20–50 n.amp, strychnine had a depressant action on neuronal activity. Firing induced by L-glutamate was