
Eve Marder and James M. Weimann

Modulatory control of multiple task processing in the stomatogastric nervous system

1.1. Introduction

Starting with the pioneering work of Don Maynard (1972), the stomatogastric nervous system of decapod crustaceans has provided numerous fundamental insights into the production of motor patterns by rhythmic neural networks. The earliest work focused on attempts to understand the neural mechanisms by which a rhythmic motor pattern can be generated (Maynard, 1972; Mulloney and Selverston, 1974a,b; Eisen and Marder, 1982; Miller and Selverston 1982a,b). Subsequently the study of the stomatogastric nervous system was instrumental in providing an understanding of the mechanisms by which neuromodulators and modulatory neurones can influence the forms of a single motor pattern (Dickinson and Nagy, 1983; Nagy and Dickinson, 1983; Hooper and Marder, 1984, 1987; Marder, 1984; Flamm and Harris-Warrick, 1986a,b; Heinzel and Selverston, 1988; Nagy et al., 1988; Nusbaum and Marder, 1989a,b; Katz and Harris-Warrick, 1990). Most recently, this preparation has allowed us to study interactions among neurones and the neural networks that together produce coordinated movements. In this chapter we will first review the evidence that demonstrates that a single group of neurones can produce multiple forms of a single motor pattern. Then we will summarise recent data which demonstrate that the same neurones can participate in the generation of several different motor patterns, and show how behavioural selection could be achieved by modulating their membrane properties and the connections between them.

The stomatogastric nervous system of decapod crustaceans controls the coordinated movements of the oesophagus and stomach (Fig. 1.1), and consists of four ganglia. There are two commissural ganglia (CGs), each consisting of several hundred neurones, a single oesophageal ganglion (OG) containing 16–18 neurones, and the single stomatogastric ganglion (STG) which consists of approximately 30 neurones. Together the neurones found in these ganglia produce at least four rhythmic motor patterns which govern the movement of food through the foregut region. Food moves from the mouth into the oesophagus (Fig. 1.1). The oesophageal rhythm has a characteristic period of 10 s, and consists of
Fig. 1.1. Diagram of the side view of the foregut region and the position of the ganglia and nerves of the stomatogastric nervous system. Abbreviations in this and subsequent figures are as follows: CG, commissural ganglion; OG, oesophageal ganglion; STG, stomatogastric ganglion; dvn, ivn, lvn, mvn, dorsal, inferior, lateral and medial ventricular nerves, respectively; pbn, pyloric dilator nerve; pyn, pyloric nerve; son, superior oesophageal nerve; sm, stomatogastric nerve.

Alternating bursts in the oesophageal dilator and constrictor motoneurones. Relatively little is known concerning the mechanisms underlying the generation of the oesophageal rhythm, although it is known that many of the oesophageal motoneurones are found in the CGs and several are found in the OG. From the oesophagus food moves into the cardiac sac region of the stomach (Fig. 1.1). The cardiac sac rhythm has a characteristic period of 30s to several minutes (Fig. 1.2). It involves motoneurones that are found in both the OG and the STG, and again relatively little is known about the pattern-generating network that underlies it.

The gastric mill receives food from the cardiac sac (Fig. 1.1). The two lateral teeth and the single medial tooth of the gastric mill shred and chew food. The gastric rhythm (Fig. 1.2) has a characteristic period of 5–10s, and is generated by neurones found in the STG. The gastric mill rhythm has been extensively studied, and is thought to be an example of a rhythmic motor pattern that depends critically for its production on emergent network properties. The pylorus is the last region of the dec-
Multiple task processing in the stomatogastric nervous system

Fig. 1.2. Motor patterns that control the movements of the foregut. Simultaneous extracellular (top two traces) and intracellular (bottom two traces) recordings. The cardiac sac rhythm is seen as slow bursts in the cardiac sac dilator 2 motoneurone (CD2) and bursts of the ivn fibres. The gastric rhythm is shown as bursts of gastric mill (GM) neurone activity recorded on the anterior lateral nerve (aLN). The pyloric rhythm is shown as rapid bursts of activity recorded in the pyloric dilator (PD) neurone. (Modified from Dickinson and Marder, 1989.)

1.2. Identification of modulatory inputs and substances

The earliest studies of the pyloric and gastric rhythms used preparations in which the STG was isolated from the more anterior ganglia of the stomatogastric nervous system by cutting either the stomatogastric nerve (stn) or the inferior and superior oesophageal nerves (ivn and ivn, respectively) (Maynard, 1972; Mulloney and Selverston, 1974a, b). Although these reduced preparations showed rhythmic activity, robust and vigorous pyloric and gastric mill rhythms are most reliably produced by preparations in which the CGs and OG are left attached (Russell, 1976, 1979; Nagy and Moulins, 1987; Hartline et al., 1988). This suggests that neurones of the CGs and OG were likely to function as modulatory inputs to the network in the STG.

The search for these modulatory extrinsic inputs to the STG took two paths. The Moulins laboratory undertook a major attempt to identify specific neurones in the CGs and OG with modulatory actions on the...
Neurobiology of motor programme selection

**Diagram**

- cCK
- FLRF
- MYOMO
- nPDH
- PROC
- RPCH
- SUB P
- ALA
- STN
- DVN

**Text**

Fig. 1.3. Diagram summarising the neuromodulatory substances found in neurone projections from the STN into the neuropil of the STG of the generic crustacean. Not all substances are found in all decapod species. Several axons in the DVN also contain GABA, proctolin, FLRFamide and 5-HT. Large clear circles show the somata of the STG. All motoneurones of the STG are either cholinergic or glutamatergic (Marder, 1987). CCK. Crustacean cholecystokinin, visualised by Turrigiano and Selverston (1989) using antibodies raised against vertebrate CCK; FLRF, FLRFamide-like peptides, visualised with antibodies initially raised against FMRFamide, see Marder et al. (1987b); MYOMO, myomodulin-like immunoreactivity, visualised using antiyomodulin, gift of K. Weiss, in unpublished experiments of Lockhart, Oshinsky, Hall and Marder; nPDH, β-pigment dispersing hormone-like immunoreactivity, visualised using anti-βPDH, gift of R. Rao, see Martin and Marder (1989, 1991); PROC, proctolin, see Marder et al. (1986); RPCH, red pigment concentrating hormone-like peptide, see Nusbaum and Marder (1988), Dickinson and Marder (1989); SUB P, substance P-like immunoreactivity, tachykinin-like substance, see Goldberg et al. (1988); ACh, acetylcholine, thought to be the neurotransmitter released by the anterior pyloric modulator (APM) neurone described in Dickinson and Nagy (1983) and Nagy and Dickinson (1983); DA, dopamine, demonstrated biochemically and histochemically, see Kushner and Barker (1983), Marder (1987); GABA, γ-aminobutyric acid, see Caesar et al. (1989), Coulé et al. (1990), Mulloney and Hall (1990); HA, histamine, demonstrated biochemically in Claiborne and Selverston (1984); 5-HT, serotonin, see Beitz et al. (1984) and OCT, octopamine, measured biochemically in Barker et al. (1979). STN (stomachogastric nerve), ALN (anterior lateral nerve), DVN (dorsal ventricular nerve).
motor programme selection

neurones of the STG. This work has been reviewed by Nagy and Moulin (1987). A complementary approach has been to identify as many as possible of the modulatory substances present in fibres that project into the STG from extrinsic sources (Fig. 1.3). This latter approach has led to the demonstration of a large number of different substances in inputs to the STG, as shown in Fig. 1.3. These include serotonin (Beltz et al., 1984), dopamine and octopamine (Barker et al., 1979; Kushner and Barker, 1983), histamine (Claiioure and Selverston, 1984), GABA (Cazalets et al., 1987; Courtois et al., 1990; Mulloney and Hall, 1990), proctolin (Hooper and Marder, 1984; Marder et al., 1986), several FMRFamide-like peptides that we know now are likely to be extended FLRFamide-like peptides (Hooper and Marder, 1984; Marder et al., 1987b), red pigment concentrating hormone (RPCH) like peptides (Nusbaum and Marder, 1988; Dickinson and Marder, 1989), crustacean cholecystokinin (CCK)-like peptides (Turrigiano and Selverston, 1989; 1990), a substance-P-like immunoreactivity (Goldberg et al., 1988), a β-pigment dispersing hormone (β-PDH)-like peptide (Morrin and Marder, 1989, 1991), and a myomodulin-like peptide (Lockhart, Hall, Oshinsky and Marder, unpublished results).

The presence of this large number of different substances in the fibres projecting into the STG clearly indicates that neural networks may be modulated by many different substances. Additionally, other substances may reach the neuropil of the STG as hormones, even if they are not found in neuronal projections to the STG. For example, crustacean cardioactive peptide (CCAP), found in neurosecretory structures in crabs and lobsters but not in direct neuropil projections (Dircks and Keller, 1988; Morin et al., 1990), has pronouced physiological actions on STG motor patterns in several species (Heinzel, Weimann, Morin and Marder, unpublished results).

1.3. Multiple forms of the pyloric rhythm

Since the pyloric rhythm is the best understood and most stereotyped of the motor patterns produced by the stomatogastric nervous system, the effects of different modulatory substances have been most extensively studied on it (Beltz et al., 1984; Hooper and Marder, 1984, 1987; Marder et al., 1986; Nusbaum and Marder, 1988; Cazalets et al., 1987). Comparison of the effects of several modulatory substances on the pyloric rhythm shows clearly that each substance produces characteristic and different motor patterns (Marder, 1984; Marder and Hooper, 1985; Flamm and Harris-Warrick, 1986a,b; Marder, 1987; Marder et al., 1987a; Harris-Warrick, 1988; Harris-Warrick and Marder, 1991). Figure 1.4 provides a comparison of the effects of eight modulatory substances on the pyloric rhythm of the crab Cancer borealis. These records come from
Fig. 1.4. Multiple forms of the pyloric rhythm induced by different neuro-modulatory substances, isolated STG from the crab, *Cancer borealis*. All panels, top trace intracellular recording from the lateral pyloric (LP) neurons; second trace intracellular recording from the pyloric dilator (PD) neuron; third trace, extracellular recording from the lateral ventricular nerve (lve). The preparation was extensively washed between each modulator application and returned to control levels of activity before new application. Concentrations: pilocarpine, $10^{-3}$M; serotonin, $10^{-4}$M; prococin, $10^{-4}$M; dopamine, $10^{-4}$M; SDN-NFLFamide, $10^{-7}$M; TNR-NFLFamide, $10^{-7}$M; CCAP, $10^{-4}$M; RFCH, $10^{-4}$M. Horizontal calibration bar, 2s. Vertical calibration bar, 10mV.

a single preparation that was extensively washed between each application. In this experiment, neural inputs from the CGs were removed and the control condition was one in which the pyloric rhythm was quiescent. The intracellular records shown in the top two traces in each panel are from the lateral pyloric (LP) and pyloric dilator (PD) motor neurones that innervate respectively the constrictor and dilator muscles of the pyloric region. Each exogenously applied substance produced a different form of the pyloric motor pattern. When applied to this quiescent preparation all of these substances were ‘excitatory’ in that they evoked an increase in firing in all cases, and, except for dopamine, induced rhythmic alternations between the PD and LP neurones. However, in each case the exact phase relationships, the intensities of the neuronal bursts, and the intracellularly recorded waveforms of the neurones were different.

Pilocarpine is a muscarinic, cholinergic agonist which is effective in initiating rhythmic pyloric activity (Marder and Paupardin-Tritsch, 1978; Marder et al., 1987a; Marder and Meyrand, 1989). In the presence of pilocarpine the pyloric rhythm was rapid and regular.
seen in serotonin, such as that shown in Fig. 1.4, are typically characterised by shallow PD membrane potential oscillations. With long LP neurone bursts that do not occur with each PD neurone burst (Belz et al., 1984; Katz and Harris-Warrick, 1990). The pyloric rhythm seen in the presence of proctolin is associated with long, high-frequency, LP neurone bursts (Marder et al., 1986). Dopamine has a strong depolarising action on both the PD and LP neurones, which, even at the modest concentration shown here (10^{-6} M), is sufficient to disrupt the burst formation of the pyloric network (see Marder and Meyrand, 1989). The extended FLRFamide-like peptides, SDRNFLRFamide and TNRNFLRFamide, evoked strong pyloric rhythms that are not unlike those seen with pilocarpine (shown just above them for comparison) in that the intensity of the bursts in the PD and LP neurones were similar. CCAP, like serotonin, shown just above it, produced rhythms in which long LP neurone plateaux alternated not with each PD burst, but with every third or fourth PD burst. The pyloric rhythms seen in RPCH most resemble those seen in proctolin (just above it) in that both proctolin and RPCH produce LP neurone activity-dominated pyloric rhythms.

1.4. Multiple forms of the gastric rhythm

Many of the modulatory substances discussed above (Fig. 1.3) also produce dramatic physiological actions on gastric motor patterns. As is the case for the pyloric rhythm, a number of different modulatory substances can activate gastric motor patterns. These include proctolin (Marder et al., 1986; Heinzle and Selverston, 1980), octopamine (Selverston et al., 1983), muscarinic agonists (Weimann, unpublished results), crustacean CCX-like peptides (Tutzig and Selverston, 1989) and FLRFamide-like peptides (Weimann and Marder, 1989; Weimann et al., 1990). Again, as is the case for the pyloric rhythm, each of the modulatory substances produces different forms of the gastric rhythm. Since the gastric rhythm is less stereotyped than the pyloric, a comparison of the full complexity of the gastric rhythms produced by the many modulatory substances shown in Fig. 1.3 has not yet been completed. However, we anticipate that systematic comparisons will yield much insight into the mechanisms controlling the different forms of gastric patterns produced.

1.5. Neurones that switch between pattern-generating networks

The pyloric, gastric, and cardiac sac rhythms can be simultaneously active, with frequencies that routinely differ by more than an order of magnitude (Fig. 1.2). For example, the pyloric rhythm is commonly found with a period of about 1 s, the gastric rhythm characteristically has a period of 5–10 s, and the cardiac sac rhythm has a characteristic period
of 30–120s. Although these circuits were classically considered to comprise distinct groups of neurones (Selverston and Moulines, 1987), it has been known for many years that there are interactions between them. In preparations from *Panulirus interruptus*, interactions between the gastric and pyloric rhythms are often seen as perturbations of the ongoing pyloric rhythm at distinct phases of the gastric rhythm (Mulloney, 1977). Cardiac sac bursts are associated with disruptions of both the pyloric and gastric rhythms (Nagy and Moulines, 1987; Dickinson and Marler, 1989; Dickinson et al., 1990). In *Homarus gammarus* modulations of robust gastric bursts occur in time with the more rapid pyloric rhythms (Robertson and Moulines, 1984). In a recent study in the lobster *Palinurus vulgaris*, Hooper and Moulines (1989) showed that sensory inputs activated by stretch could switch the ventricular dilator (VD) neurone, which usually functions as part of the pyloric network, into cardiac sac motor patterns. In this case, sensory activation switches the VD neurone between two ongoing motor patterns, and the mechanism underlying the switch is a change in the extent to which the VD neurone expresses plateau properties (Hooper and Moulines, 1989).

In the crab *Cancer borealis*, many neurones switch between ongoing pyloric and gastric motor patterns. In this species neurones can display either gastric-timed or pyloric-timed activity patterns depending on the modulatory environment (Weimann et al., 1990, 1991). In preparations that show only rapid, pyloric rhythms, all of the neurones that are classically considered part of the pyloric circuit participate in the pyloric rhythm. Under these conditions many of the neurones usually classified as gastric neurones also fire in time with the pyloric rhythm. In the top set of recordings shown in Fig. 1.5, the lateral gastric neurone (LG) fires with the pyloric rhythm. However, when the gastric rhythm is activated, as can occur either spontaneously or after the application of the extended FLRFamide-like peptide, SDRNFLRFamide (Weimann et al., 1989, 1990), most of the gastric neurones display gastric rhythm timed activity, and some of the neurones usually considered part of the pyloric circuit show gastric-timed activity (Weimann et al., 1990, 1991). The middle panel in Fig. 1.5 shows a recording from an LG neurone in a hybrid gastric/pyloric pattern associated with weak gastric activity (monitored on the dgn). The bottom trace in Fig. 1.5 shows that the LG neurone can produce a full gastric motor output with little obvious pyloric modulation during robust gastric mill activity.

In many situations, e.g. walking and swimming in man, the same motoneurones are active during different behaviours. In most cases these motoneurones are not part of the pattern-generating circuits but are simply driven by whichever pattern generator is active. However, in the STG, the motoneurones themselves, together with several interneurones, make up the pattern-generating networks. Therefore, the stomatogastric
basically considered to command and Moulins. 1987), it has interactions between them. In interactions between the gastric activities of the ongoing pyloric (Mulloney. 1977). Cardiac both the pyloric and agas- kinson and Marder. 1989: cardiac modulations of robust gas- pyloric rhythms (Robertson of the lobster Palinurus vulgaris. sensory inputs activated by T/D neuron, which usually cardiac sac motor patterns. VD neuron between two underlyings the switch is a neuron expresses plateau pro- modes switch between ongoing species neurons can display patterns depending on the 1990, 1991). In preparations the neurons that are classi- it participate in the pyloric neurons usually classified as tonic rhythm. In the top set of gastric neuron (LG) fires with gratic rhythm timed activity, as application of the extended de (Weimann et al., 1989, gastric rhythm timed activity, ed part of the pyloric circuit cat., 1990, 1991). The middle an LG neuron in a hybrid gastric activity (monitored on shows that the LG neuron can de obvious pyloric modulation swimming in man, the same behaviours. In most cases these generating circuits but ar. tor is active. However, in the toer with several interneurons. Therefore, the stomatogastric

---

Fig. 1.5. Neurons that switch between gastric and pyloric activity patterns. Top panel: in the absence of an ongoing gastric rhythm (no activity in the dorsal gastric (DG) neuron) the lateral gastric (LG) (one of the 'gastric' neurons) fires in time with the pyloric rhythm (shown as the activity pattern in the LP neuron). Middle panel: during weak gastric activity (see activity of the DG on the dpn), the LG fires in a hybrid pattern, with pyloric timed hyperpolarisations interspersed with longer period short bursts. Bottom panel: during robust gastric activity, seen as the dense DG bursts on the dpn, the LG neuron now fires in intense gastric bursts and shows little pyloric modulation. Horizontal calibration bar is 5s for the top and bottom panels and 2.5s for the middle panel. The vertical calibration bar is 18 mV for the LG and 20 mV for the LP neuron in the first two panels; 26 mV for LG and 18 mV for the VD neuron in the bottom panel.
ganglion serves as a model system only for those central networks that directly produce behaviours. As the motoneurones in the crab STG change from gastric-timed to pyloric-timed activity patterns, these changes have important consequences for the operation of the pattern-generating networks in which these neurones function. We have recently shown (Weimann and Marder, unpublished results) that ‘gastric’ neurones not only can fire in pyloric time, but also can reset the pyloric rhythm. Likewise, ‘ pyloric’ neurones can fire in time with the gastric rhythm, and can also reset the gastric rhythm. This ability to reset the ongoing rhythmic motor pattern is one of the classical experimental demonstrations that identify a neurone as part of the circuit responsible for the generation of the rhythm. Thus, these data argue that all of these neurones have access to the pattern-generating circuitry for both rhythms, and participate at all times to a greater or lesser degree in shaping both rhythms.

The mechanisms responsible for the pyloric/gastric transitions such as those shown in Fig. 1.5 are complex. Preliminary experiments show that some of the peptide-induced changes are associated with inductions of plateau properties in single neurones such as the DG neurone and modifications of defined synaptic interactions (Weimann et al., 1990). The firing patterns of each cell will be uniquely controlled by its membrane properties and the strength of the synaptic contacts at any moment in time. Therefore, it is likely that each ‘switch’ (i.e. the selection of each motor pattern) is associated with a different pattern of modification in synaptic efficacy and cellular properties.

1.6. Gastric/cardiac sac fusion

Unlike the previous cases in which neurones change their allegiance between two ongoing rhythmic motor patterns, in *Panulirus interruptus* the neuropeptide, RPCH, ‘fuses’ two motor patterns into one (Dickinson, 1989; Dickinson et al., 1990). Figure 1.2 shows that in control saline the cardiac sac and gastric motor patterns operate simultaneously but with different frequencies. However, in the presence of RPCH, cardiac sac and gastric motor neurones fire in a single alternating motor pattern (Fig. 1.6) which is neither a true cardiac sac pattern nor true gastric pattern. In the example shown in Fig. 1.6, note that cardiac sac CD2 motoneurone and the ivn fibres (also part of the cardiac sac system) fire together in alternation with the gastric mill (GM) and lateral posterior gastric (LPG) motoneurones of the gastric system. Thus, here we see that elements of two initially separate neural circuits have been combined to produce a single conjoint rhythm.

In this case the mechanism responsible for the production of this conjoint rhythm is an RPCH-induced potentiation of the synaptic poten-
Multiple task processing in the stomatogastric nervous system

ivN

GM

LPG

CD2

3 sec

15 mv

Fig. 1.6. Novel pattern shown by gastric/cardiac sac neurons in the presence of the peptide RPCH. Under control conditions the cardiac sac and gastric motor patterns cycle independently at different frequencies, as shown in Fig. 1.2. In the presence of RPCH the two networks are ’fixed’ and produce a single rhythmic motor pattern in which CD2 and gastric motoneurons (GM and LPG) fire in alternating bursts. (Modified from Dickinson et al., 1990.)

...
Fig. 1.7. Networks are multiple task processors (MTPs). (A) Different modulatory substances can produce different output patterns from a single subsystem. The block diagrams are a cartoon representation of the phase of the pyloric rhythms seen following bath application of the different modulatory substances. (B) Modulatory substances can 'fuse' two relatively independent subsystems, as represented by circles and triangles, into a single functional unit (squares), which produces a novel conjoint rhythm with a period and element phases different from either of the starting subsystem outputs. (C) Modulatory inputs can select multiple network constellations from a group of neurons (circles), resulting in neurons 'switching' to produce different output patterns. Three of the many types of network configuration are shown with the circles, triangles and squares representing different activity patterns.
vary, burst durations vary, and burst intensities vary (Fig. 1.4, Fig. 1.7A). These kinds of changes might be employed as an animal adopts an ongoing locomotory rhythm to slight modifications of load or terrain. Although many of the changes of this sort can be quite dramatic and might have profound behavioural consequences, we have become accustomed to thinking that they must occur to enable animals to adapt to environmental changes.

The changes illustrated in Figs 1.7B and 1.7C require us to re-evaluate many of our current ideas about the definition of central neural networks. Some neurones may be found in neural subsystems which can be operated either independently or combined with other subsystems to produce different behaviours such as the conjoint rhythms elicited by RPCH (Figs 1.6, 1.7B). Neurones may be found in neural networks that exist in complicated patterns of connectivity where many of the synaptic and cellular properties are subject to modulation. In this case, a modulatory substance might activate neurones and synaptic pathways to form a new functional network. This is diagrammatically shown in Fig. 1.7C, where the individual elements in the unmodulated state are shown as circles. For example, one modulatory substance may elicit pyloric-timed activity in some neurones (squares) and gastric-timed activity in others (triangles). Different modulatory substances might 'select' other neurones and other pathways from the constituent ensemble to form new active circuits (Fig. 1.7C). The organisation shown in Figs 1.7B and 1.7C can lead not only to modifications in frequency and phase, such as illustrated in Fig. 1.7A, but also to neurones switching between two ongoing rhythms to form different operationally defined circuits, rhythmic or otherwise, as illustrated in Figs 1.7B,C. This idea is attractive in that it allows an anatomically defined, synaptically coupled network to perform multiple tasks, some of which can occur simultaneously, others of which may only occur sequentially.

In summary, we now argue that modulatory inputs may allow us to understand how biological 'wetware' can act as a multiple task processor (MTP). Modulatory substances 'program' the MTP by selecting or activating neurones from the ensemble and by changing the gain of the synaptic connections in the ensemble. Although the elements and connections 'selected' serve as the resident 'program', it is important to remember that even non-responsive or silent neurones can have important consequences for circuit operation (Hooper and Marder, 1987; Kepler et al., 1982).

In a nervous system operating as a multiple task processor, a given neurone may operate at different times in entirely different roles in different, functional, neural circuits. The phenotype of such neurones would be that they would 'switch' their activity patterns, but a full understanding of the extent to which they subserve different roles will require
far more complete knowledge about the organisation of the neural networks underlying behaviour than is currently available in any preparation. Despite the extensive modulation of networks described in this chapter, network operation in animals seems rarely compromised by 'overmodulation' (Marder and Meyrand, 1989). Thus, an important challenge for the future will be to understand both how network structure constrains the inherent flexibility produced by multiple modulatory processes and how modulation itself is controlled. Research on the changes produced by modulatory substances and neurones in the stomatogastric nervous system should allow us to understand more fully the detailed mechanisms underlying the kinds of modulatory change described in this chapter and to aid our understanding of the selection of motor patterns. We anticipate that similar results will be forthcoming in other nervous systems as the neural networks that produce and control behaviour become better described.

Acknowledgements

We thank Ms Elizabeth Orban, Ms Cassandra Hall and Mr Michael O’Neil for help with figure preparation. Discussions with Drs Patsy Dickinson, Scott Hooper and Pierre Meyrand were critical in the formulation of many of these ideas. Research was supported by NS 17813.

References


Multiple task processing in the stomatogastric nervous system


Marder, E., Calabrese, R. L., Nusbaum, M. P. and Trimmer, B. (1987b). Distribution and partial characterization of FMRFamide-like peptides in the...


Multiple task processing in the stomatogastric nervous system


