Oscillatory Neural Networks: an Evolutionary Perspective

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Abstract

Motor patterns of the stomatogastric ganglion neurons of the shrimp Penaeus japonicus were studied in semi-isolated preparations of the complete stomatogastric nervous system. The oscillatory neural network can generate flexible motor patterns under the influence of extrinsic inputs from the higher center. Some neurons of the pyloric network are enhanced in their burstiness by excitatory synaptic input from the brain. They construct the cardiac sac pattern generator together with the cardiac sac dilator neurons. The gastric-pyloric pattern is organized by coordination between inputs from the commissural ganglia and their target neurons in the STG. Complete cessation of the pyloric rhythm results in turning on the gastric rhythm. Proctolin and octopamine of neuromodulators can initiate the gastric rhythm. Neurons of the STG provide part of a single neural network from which they can be assembled for configuration of the pattern generators under the appropriate modulatory conditions. Comparative analyses of the stomatogastric system have been made for understanding evolutionary trends of the peripheral motor system and the central neural network.

Key Words: stomatogastric ganglion, oscillatory neural network, synaptic input

INTRODUCTION

The stomatogastric nervous system (STNS) of decapod crustaceans is an important center for coordinated movements of the foregut. The STNS consists of the paired commissural ganglia (CoGs), the oesophageal ganglion (OG), the stomatogastric ganglion (STG), and the nerves connecting these ganglia. The STG contains the pattern-generating networks for movements of the three distinct regions of the foregut: the cardiac sac, gastric mill and pylorus (Selverston and Moulins, 1987; Harris-Warrick et al., 1992a). The STG has approximately 30 cell bodies, most of which are motor neurons that participate in either the gastric or pyloric motor patterns (Maynard, 1972). Approximately one-half of these neurons are components of the gastric network, and about one-half are part of the pyloric network. The STG also contains the cell body of the cardiac sac motor neuron. Most of the neurons in these networks are capable of generating endogenous oscillatory potentials that are important for the production of rhythmic motor patterns (Russell and Hartline, 1978, 1982). The neurons identified in the higher center (Brain, CoGs and OG) contain a variety of modulatory substances that can profoundly influence the gastric and pyloric motor patterns (Harris-Warrick and Marder, 1991; Harris-Warrick et al., 1992b). The neural networks in the STG are multifunctional due to a number of neuromodulatory inputs.

The most extensive study of the STNS has been performed on the spiny lobster Panulirus interruptus (infraorder Palinura). Other decapod species such as clawed lobsters Homarus americanus and Homarus gammarus (infraorder Astacidea) and crabs Cancer borealis and Cancer pagurus (infraorder Brachyura) have also been employed for the stomatogastric research (Katz, 1991; Katz and Tazaki, 1992). All these species belong to the most advanced decapod group, Reptantia (Abele and Felgenhauer, 1986). The STNS of the penaeidean shrimp Penaeus japonicus has been studied from a comparative perspective (Tazaki and Tazaki, 1997, 2000). This non-reptantian genus belongs to the most primitive decapod group, Dendrobranchiata (Abele and Felgenhauer, 1986).
The crab Cancer is characterized by a complex organization of the foregut, whereas the shrimp Penaeus is characterized by a simple organization (Maynard and Dando, 1974; Meiss and Norman 1977a, b). The foregut of the shrimp Penaeus represents the most primitive decapod foregut (Felgenhauer and Abele, 1989; Lovett and Felder, 1989). There is a gastric mill that appears to be small denticles rather than cutting and grinding structures as seen in reptantians. In the shrimp Penaeus, the pyloric network is similar to the homologous network of other decapod species examined (Tazaki and Tazaki, 1997), and neurons of the STG construct a multifunctional neural network (Tazaki and Tazaki, 2000).

The present study provides modulation of motor patterns by neural inputs projecting to the oscillatory neural network in the STG to address questions how motor systems have evolved to produce new movements. Spontaneous activity was recorded from STG neurons in the STNS of the shrimp Penaeus japonicus. Excitatory synaptic input from the brain enhanced burstiness in some neurons of the pyloric network to construct the cardiac sac pattern generator, together with the cardiac sac dilator neurons. The pyloric pattern was organized with the commissural pyloric and the pyloric pacemaker neurons. Complete cessation of the pyloric pattern resulted in generation of the gastric pattern. Some neurons in the pyloric and the gastric network moved from one pattern generator to another. Proctolin and octopamine could initiate the gastric pattern. By phylogenetically comparing the stomatogastric system in different decapod infraorders, it may be possible to understand how the neural network was modified in the course of evolution and which components were conserved and which were varied.

MATERIALS AND METHODS

Experiments were performed on the STNS of the shrimps Penaeus japonicus. Animals were maintained in a tank of recirculating artificial sea water at 20°C until used.

The STNS is shown in Fig. 1. The STG is connected to the paired CoGs and the single OG by a single nerve tract, the stomatogastric nerve (stn) that contains descending axons of neurons located in the brain, CoGs and OG. The paired superior oesophageal nerves (son) emerging from each CoG join the stn. The paired inferior oesophageal nerves (ion) connect each CoG with the OG. The inferior ventricular nerve (ivn) from the brain joins at the OG. Several motor nerves emerging from the STG carry motor axons, and innervate foregut muscles. The semi-isolated preparation of the complete STNS was dissected out. The preparation was continuously superfused with Penaeus saline (Tazaki and Tazaki, 1997) at room temperature (20-26°C). Spontaneous activity was recorded intracellularly from the neuronal somata in the desheathed STG, and extracellularly from the peripheral nerves. Electrophysiological techniques were standard to our laboratory. Proctolin or octopamine (purchased from Sigma) was mixed immediately before use from frozen stock solutions. Methods of identification of neuronal somata in the STG have been described in the previous paper (Tazaki and Tazaki, 1997). All experiments were repeated at least three times.

RESULTS

Oscillatory neural networks

Both the synaptic connectivity among neurons in the STG and the oscillatory property of individual neurons are important for understanding full range of motor patterns produced by the STNS in the shrimp Penaeus japonicus (Tazaki and Tazaki, 2000). A connectivity diagram is shown in Fig. 2. The chemical inhibitory synapses organize constituent neurons into reciprocally inhibitory loops. Some neurons are electrically coupled to produce synchronous activity between them. The discrete pyloric and gastric networks are remarkably similar to those examined in the lobster Panulirus (Mulloney, 1987). This wiring diagram is relevant to analyses of generation of multiple motor patterns. The oscillatory property of neurons is characterized by capability of producing regenerative plateau potentials underlying bursts (Russell and Hartline, 1978, 1982). Most of the STG neurons are endowed with such regenerative properties whose expression are synaptically induced by neural inputs (Hartline and Graubard, 1992).
Oscillatory neural networks

Fig. 2. Synaptic connectivity among STG neurons. Pyloric and gastric networks. Electrically coupled neurons are drawn in the same circle or connected by a resistor symbol. Black circles represent chemical inhibitory synapses; white circles functional inhibitory interaction not known to be monosynaptic. There are interconnections between the pyloric and the gastric network. Cardiac sac network has not been established. Abbreviations: AB, anterior burster neuron; AM, anterior median neuron; DG, dorsal gastric neuron; GM, gastric mill neuron; IC, inferior cardiac neuron; Intl, interneuron 1; LG, lateral gastric neuron; LP, lateral pyloric neuron; LPG, lateral posterior gastric neuron; MG, median gastric neuron; PD, pyloric dilator neuron; PY, pyloric neuron; VD, ventricular dilator neuron. Nomenclature was taken from Maynard and Dando (1974). (Modified from Tazaki and Tazaki, 2000)

Motor patterns

In semi-isolated preparations of the STNS of the shrimp *Peneaus*, the pyloric system usually operated to produce spontaneous rhythmic output. The gastric system often operated, and the cardiac sac system occasionally operated. These systems generate three different rhythmic motor patterns that are spontaneously produced by intrinsic oscillatory properties of their constituent neurons.

The cardiac sac network is incompletely characterized, largely because it is distributed across several ganglia. The cardiac sac dilator 1 (CD1) neuron, with its cell body in the OG, and the cardiac dilator 2 (CD2) neuron, with its cell body in the STG, participate in the cardiac sac rhythm (Dickinson and Marder, 1989). The ivn fibres are another component of the cardiac sac pattern. The cardiac sac pattern is shown in Fig. 3A. The CD2 neuron fired rhythmic bursts with a period of approximately 10 sec. The ivn fibres also fired bursts of high-frequency axonal spikes corresponding to CD2 bursts. The cardiac sac cycle has periods of 5 to 20 sec.

The gastric pattern is shown in Fig. 3B. The dorsal gastric (DG) and gastric mill (GM) neurons fired alternately with a period of 6 sec. In this preparation the pyloric rhythm was quiescent as illustrated in the motor nerve lvn where axonal spikes of some pyloric neurons were observable. As shown in the gastric network of Fig. 2, the DG neuron fires together with the anterior median (AM) neuron, being in phase with the interneuron 1 (Intl). The lateral gastric (LG) and median gastric (MG) neurons fire at approximately the same time, being in antiphase with the DG·AM and Intl neurons, and alternate with the lateral posterior gastric (LPG) neurons. The gastric cycle has periods of 5-10 sec.

The pyloric pattern is shown in Fig. 3C. The pyloric dilator (PD) and pyloric (PY) neurons fired alternately with a period of 1.2 sec. In this preparation, the pyloric rhythm was silent as illustrated in the motor nerve lvn where axonal spikes of some pyloric neurons were observable. As shown in the pyloric network of Fig. 2, the PD neuron organizes the pyloric rhythm together with the anterior burster (AB) neuron that is an interneuron of the pyloric network. The lateral pyloric (LP), inferior cardiac (IC), and ventricular dilator (VD) neurons are members of the pyloric network. Activities of PD·AB neurons initiate the pyloric cycle, and then bursts of

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**Fig. 3.** Cardiac sac, gastric, and pyloric motor patterns. Intracellular activities recorded from the neuron somata. Extracellular axonal spikes monitored from the nerves indicated. A Cardiac cycle. The CD2 neuron fires rhythmic bursts with a period of 10 sec, together with the ivn. B Gastric cycle. The DG and GM neurons fire alternately with a period of 6 sec, being in antiphase with the LG and MG neurons. C Pyloric cycle. The PD and PY neurons fire alternately with a period of 1.2 sec.
The pyloric rhythm has periods of 0.5-2 sec. The cardiac sac, gastric, and pyloric pattern generators generally function as separate neural networks when they are active. However, there are so many interconnections between neurons in these networks that they construct the multifunctional neural network (Fig. 2). Since these neurons were under the influence of neural inputs from the higher center, multiple motor rhythms were observable. Several extrinsic neurons that synapse with STG neurons have been identified (Mulloney, 1987). The present experiments were undertaken to show how extrinsic synaptic inputs modulate activities of various cell types of neurons in the STG.

Inferior ventricular neurons

The nerve inn from the brain joins at the OG (Fig. 1). The cell bodies of inferior ventricular (IV) neurons are located in the brain, and their axons travel in the inn, through the OG and down the sin to the STG (Claiborne and Selverston, 1984). The IV neurons are components of the cardiac sac motor pattern (Fig. 3A), and they make excitatory synapses with some of the STG neurons (Mulloney, 1987). Figure 4A shows the cardiac sac motor pattern intracellularly recorded from the CD2 neuron that projects its axon down the sin and son. The PY neuron repeated with the pyloric rhythm (Fig. 4A1), firing alternately with the PD neuron (illustrated in the inn trace). The CD2 neuron generated sustained bursts of spikes that were associated with axonal spikes in the nerve son (Fig. 4A2). Excitatory postsynaptic potentials (EPSPs) evoked by the IV neurons occurred in the PY neuron at approximately the same time as CD2 firing. The PY neuron was strongly inhibited during the CD2 firing phase. Prolonged bursts corresponding to CD2 bursts were also observable in the motor nerve inn.

The PD neuron receives excitatory input from the IV neurons. The motor pattern of PD neuron was recorded in the same preparation. The PD and PY neurons fired alternately with the pyloric rhythm (Fig. 4B1). When IV-evoked EPSPs occurred in the PD and PY neurons, the PD neuron provoked long plateaus of firing that were associated with bursts of high-frequency axonal spikes in the motor nerve inn (Fig. 4B2). The CD2 neuron was also active as seen in the nerve son. Enhancement of burstiness in the PD neuron resulted in strong inhibition of the PY neuron. The hyperpolarization caused the PY neuron to depolarize abruptly after termination of PD firing, leading to resumption of bursting. The PD neuron fires in phase with the CD2 neuron by synaptic activation.

![Figure 4: Excitatory input from the IV neurons](image)

**Fig. 4.** Excitatory input from the IV neurons. Intracellular activities recorded from the neuron somata. Extracellular axonal spikes monitored from the inn and son. **A1** Activities of the CD2 and PY neurons. PY fires with the pyloric rhythm, alternating with PD. **A2** CD2 generates sustained bursts. EPSPs evoked by the IV neurons occur in PY during the CD2 firing phase, and PY discharges are shut off. **B1** Activities of the PD and PY neurons. PD and PY fire with the pyloric rhythm. **B2** EPSPs are evoked in PD and PY. PD bursting is promoted to produce plateaus of firing. PY discharges are inhibited by strong hyperpolarization evoked by PD. A and B are from the same preparation.
Oscillatory neural networks

The VD neuron could switch from the pyloric to the cardiac sac pattern. Intracellular recordings were made from the PD, VD and PY neurons. The PD neuron fired alternately with the PY and VD neurons (Fig. 5A1). A brief pulse of 0.1 msec duration with moderate intensity was delivered to the ivn during their spontaneous discharges. Continuous stimulation of the ivn at 15 Hz evoked repetitive EPSPs (illustrated in the PY trace), and promoted burstiness in the PD neuron (Fig. 5A2). The VD neuron fired bursts of spikes, being in phase with the PD neuron. Promotion of burstiness in the PD and VD neurons is a long-lasting effect that vanished at several tens of seconds after the ivn stimulation. The VD neuron also receives excitatory input from the IV neurons. Under the influence of excitatory input, the PD and VD neurons can switch their allegiance from the pyloric network to participate in a cardiac sac pattern generator.

The LPG neuron is electrically coupled to the PD·AB and VD neurons, and is mostly active in time with the pyloric rhythm (Tazaki and Tazaki, 1997). The effect of the ivn input on the LPG neuron was examined (Fig. 5B1). The LPG neuron was active in time with the pyloric rhythm, firing spikes on slow oscillatory potentials that was synchronous with PD bursts due to strong electrical coupling between them (Fig. 5B1). Continuous stimulation of the ivn at 10 Hz promoted burstiness in the PD neuron, whereas it inhibited the production of slow oscillatory potentials in the LPG neuron (Fig. 5B2). Strong electrical coupling that maintains the activity of the LPG neurons synchronous with the PD·AB neurons appears to be modulated under the influence of the ivn input. In spite of inhibition by the ivn input, however, small EPSPs were evoked in the LPG neuron during its sustained inhibitory responses. The LPG neuron may receive excitatory and inhibitory inputs from the IV neurons. In these excitatory and inhibitory synapses, synaptic efficacies of the target neurons may be modified under the influence of neuromodulators.

CoG neurons

In the lobster Panulirus, the paired CoGs contain the commissural pyloric (CP) neurons that send excitatory input to pyloric neurons to induce a robust pyloric rhythm, due to the induction of endogenous bursting properties in the AB neuron (Mulloney, 1987). Since the CP neurons receive inhibition from the AB neuron to operate as a feedback loop, they can entrain the pyloric rhythm. Equivalent CP neurons are found in the shrimp Penaeus. An example of interactions...
between the CP and the AB neuron is shown in Fig. 6A. Oscillatory plateau potentials of the AB neuron were preceded by a high-frequency train of EPSPs evoked by the CP neurons (Fig. 6A1). These EPSPs disappeared after AB firing. The axons of CP neurons travel in the son, and down the stn to the STG (Mulloney, 1987). A brief pulse of 0.1 msec duration with moderate intensity was delivered repetitively to the son to evoke EPSPs in the AB neuron. Continuous stimulation of the son at 30 Hz caused the AB neuron to accelerate and intensify its bursting activity (Fig. 6A2).

An example of interactions between the CP and the pyloric neurons is shown in Fig. 6B. The AB and PY neurons fired alternately. Oscillatory plateau potentials of the AB neuron were preceded by CP-evoked EPSPs (Fig. 6B1). When the AB neuron ceased to oscillate due to the reduction of CP firing as seen in a low-frequency train of EPSPs, the PY neuron fired gastric-timed bursts (Fig. 6B2). When the pyloric rhythm in the AB neuron resumed, the PY neuron followed its rhythm. The oscillatory activity of the AB neuron induced by the CP neurons can maintain rhythmic motor output from the pyloric network.

In the lobster Panulirus, the paired CoGs contain the commissural gastric (CG) neurons that send excitatory input to gastric neurons to reinforce the oscillatory tendency of the corresponding neurons (Mulloney, 1987). Equivalent CG neurons are found in the shrimp Periclimenaeus. An example of interactions between the CG and the gastric neurons is shown in Fig. 6C. The LPG neuron fired bursts in phase with the PD and AB neurons (illustrated in the lvn and son traces), and the MG neuron received inhibition from the AB and LPG neurons (Fig. 6C1). When CG-evoked EPSPs occurred in these neurons, they became active in time with the gastric rhythm (Fig. 6C2). The pyloric rhythm was turned off because of complete cessation of AB firing. Other gastric neurons (LG and GM) also fired with the gastric rhythm as illustrated in the lvn trace. The LPG and
MG neurons can switch into the gastric pattern in the absence of the pyloric rhythm and under modulation of the CG neurons. The observation of Fig. 6 indicates that neurons of the gastric and pyloric networks can configure a gastric-pyloric pattern generator.

Pyloric oscillator neuron

The AB neuron is the fastest oscillator of the pyloric network that organizes the pyloric pattern together with the CP neuron (Mulloney, 1987). In the shrimp Penaeus, all of the gastric neurons can be active in time with the pyloric rhythm (Tazaki and Tazaki, 2000), unlike those in the crab Cancer where the DG neuron fires exclusively with the gastric rhythm and other gastric neurons can fire with the pyloric rhythm (Weimann et al., 1991). The reduction or complete cessation of pyloric pattern can change activity patterns of the pyloric and gastric neurons.

The gastric neurons could change their activity patterns by inactivating the pyloric pacemaker neuron. An example of motor patterns is shown in Fig. 7. The pyloric AB neuron inhibits the gastric MG neuron (Fig. 2). The MG neuron fired alternately with the AB neuron (Fig. 7A). Sustained hyperpolarizing current (-6 nA) was injected into the AB neuron soma to displace the resting membrane potential by -30 mV. The pyloric pattern was completely ceased by hyperpolarization as seen in the motor nerve dvn. The MG neuron was released from the pyloric rhythm and became active in time with the gastric rhythm. Other gastric neurons also fired with the gastric rhythm as illustrated in the dvn trace. The pyloric cycle resumed after hyperpolarization of the AB neuron was ended. In contrast, membrane potential manipulations inactivating the MG neuron could not influence the pyloric rhythm of the AB neuron (Fig. 7B). The AB neuron not only organizes the pyloric pattern but also strongly affects the gastric neurons to be active in time with the pyloric rhythm. Interconnections between neurons of the pyloric and the gastric network in the shrimp Penaeus are so extensive that they may construct a single neural network. This feature is a striking difference between the Penaeidea and the Reptantia, and is important for comparative analyses of the stomatogastric motor system.

Effects of neuromodulators on motor patterns

Many modulatory substances released from neurons located in the higher center have been identified using immunocytochemical techniques in the reptantian STNS (Harris-Warrick and Marder, 1991; Harris-Warrick et al., 1992b). These substances profoundly influence motor patterns generated by the network neurons in the STG. Effects of proctolin and octopamine on motor patterns of STG neurons were examined in the STNS of the shrimp Penaeus.

The peptide, proctolin, has been found in several modulatory neurons in the CoGs and OG (Marder et al. 1986). Figure 8A shows intracellular activities of the LPG and MG neurons that form a reciprocally inhibitory loop in the gastric network. The LPG and MG neurons fired alternately with the pyloric rhythm (Fig. 8Ai). When proctolin was bath-applied at the concentration of 10^{-7} M, the gastric rhythm was turned on. The LPG neuron alternated with the MG neuron with a period of 7 sec, although they retained a tendency to remain active in the pyloric rhythm (Fig. 8A2). The gastric rhythm became less active after washing with saline, and could be reversibly activated by proctolin (not shown).

The biogenic amine, octopamine, has been localized to axons entering the STG (Barker et al., 1979). Intracellular activity of the DG neuron is shown in Fig. 8B. In this preparation, the DG neuron was active in time with the pyloric rhythm, firing single spikes (Fig. 8Bi). The pyloric network was active as seen in the motor nerve dvn. When 10^{-4} M
Fig. 8. Effects of neuromodulators, proctolin and octopamine, on the gastric neurons. Intracellular activities recorded from the neuron somata. Extracellular axonal spikes monitored from the nerves indicated. A1 Activities of the LPG and MG neurons. LPG and MG fire alternately with the pyloric rhythm. A2 Proctolin at the concentration of $10^{-7}$ M initiates the gastric rhythm in LPG and MG that remain active with the pyloric rhythm. B1 The DG neuron fires single spikes with the pyloric rhythm. B2 Octopamine at the concentration of $10^{-3}$ M initiates the gastric rhythm in DG.

eoctopamine was applied to the preparation, the DG neuron generated rhythmic gastric-timed bursts (Fig. 8B2). The LG and MG neurons were also activated, firing in antiphase with the DG neuron as illustrated in the motor nerve Ivn. The effect of octopamine was reversible (not shown). The observation of Fig. 8 indicates that both proctolin and octopamine promote configuration of the gastric network.

DISCUSSION

In the STNS of reptantians, neurons in the STG have been classified as members of the cardiac sac, the gastric and the pyloric network due to innervation patterns of muscles in the foregut (Maynard and Dando, 1974). The gastric and pyloric networks are characterized by wiring diagrams that partially explain the motor patterns (Mulloney, 1987). Since these network neurons are under the influence of neural inputs from the higher center, synaptic strengths and intrinsic cellular properties can be extremely modified in the presence of neuromodulators (Harris-Warrick et al., 1991; Harris-Warrick et al., 1992b). The same neuron can switch from one network to the other to change its activity patterns (Hooper and Moulins, 1989; Dickinson and Marder, 1989). Thus, the pattern generating-networks are reconfigured under appropriate modulatory conditions (Dickinson and Moulins, 1992).

In the penaeidean shrimp Penaeus, all the cell types of neurons in the STG have been identified, and the gastric and pyloric networks have been elucidated (Tazaki and Tazaki, 1997). Our knowledge about configurations of the multifunctional neural networks in the STNS of the reptantians has been extended to the penaeidean shrimp Penaeus, the most primitive decapod group (Tazaki and Tazaki, 2000).

Configuration of neural networks

As shown in Fig. 2, there are extensive interconnections between neurons in the pyloric and the gastric network. Neurons of the STG provide part of a single neural network that generates many distinct motor patterns. An example of the network configuration is shown in Fig. 9. As described in Figs. 4, 5 and 6, multiple neurons move from one pattern to the other under the influence of different modulatory inputs. Neurons from a single neural network can be assembled for configuration of the pattern generators underlying motor behaviour. The IV neurons in the brain may organize the cardiac sac pattern generator. The CP and CG neurons in the paired CoGs are coordinated with the pyloric and the gastric rhythm, respectively (Mulloney, 1987). This coordination is accomplished by descending and ascending axons in the sn and son connecting the CoGs with the STG. This diagram represents interactions between inputs and their targets, and can serve as basic neural networks for the generation of multiple motor patterns in the STNS of decapods.

Many neuromodulators have been identified in the STNS, including four amines and nine neuropeptides (Harris-Warrick et al., 1992b). These substances released from the modulatory neurons cause long-lasting changes in the membrane properties and the synaptic efficacies of their targets. Exogenously applied modulators often mimic the effects of neurally released substances. Proctolin and octopamine initiate

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Figure 9. Diagrammatic view of the network configuration. Multiple neurons move from one pattern to the other. Neurons from a single neural network can be selected to make up different pattern generators under the influence of different inputs from the higher center. Excitatory synapses are made by the IV, CP and CG neurons with neurons in the STG. Inhibitory synapses are made by the interneurons (AB and Int) with neurons in the CoG. Black circles represent chemical inhibitory synapses; black triangles chemical excitatory synapses. Other symbols are defined in the legend of Fig. 2. The synapses between STG neurons are omitted. Abbreviations: CG, commissural gastric neuron; CP, commissural pyloric neuron; IV, inferior ventricular neuron.
the gastric rhythm in the shrimp *Penaeus*, as in the lobster *Panulirus* (Selverston *et al*., 1982; Heinzel and Selverston, 1988). The presence of many modulators may ensure an enormous variety of motor patterns underlying behaviour.

Evolutionary trends of motor systems

The most primitive decapod genus, the shrimp *Penaeus*, has been employed for understanding evolutionary trends of the STNS (Tazaki and Tazaki, 1997, 2000). Various features of the stomatogastric motor system can be compared across a variety of decapod species to provide evidence for what types of changes occur in the motor system during the course of evolution. The STNS of a stomatopod *Squilla*, a member of a more primitive crustacean subclass, has also been studied (Tazaki, 1993; Tazaki and Chiba, 1994, 1995).

Comparative analyses of the motor system

The basic form of the STNS and its component neurons have been strongly conserved during evolution (Katz and Tazaki, 1992; Tazaki and Tazaki, 1997). On the other hand, the gastric mill teeth are among the most phylogenetically variable feature of the stomatogastric motor system. The foregut of the mantis shrimp *Squilla* is not equipped with such a chewing apparatus as the gastric mill in decapods (Tazaki, 1993). In decapods, phylogenetic changes in the number of muscles and innervation pattern of muscles have occurred as the gastric mill has become complex during the course of evolution (Meiss and Norman, 1977a, 1977b). The Brachyura (Cancer) have the most complex motor system. Next in order of complexity is the Anomura (Pagurus) followed by the Astacidea (Homarus) and the Palinura (Panulirus). The Penaeidea (Penaeus) have the simplest type of motor system. Since a graded series of the motor system follows the evolution of the Decapoda, the peripheral motor apparatus has evolved faster than the central networks that are relatively stable due to ancestral constraints.

Some characteristics of the stomatogastric motor system are due to ancestry. Other traits are the result of adaptations to specific life-styles and diets of different decapod species (Felgenhauer and Abele, 1989). Natural selection seems to have the greatest effect on the most peripheral structures, the gastric mill teeth. Differences in structures of the gastric mill teeth have been correlated with the diet of closely related species (Kunze and Anderson, 1979). Macrophagous predatory species have stouter lateral teeth than detritus feeders. A notable feature that characterizes some species of the Reptantia is their large size compared to other decapods. The development of the gastric mill as an efficient triturating device may have been a new style that allows large decapods to exploit the feeding behaviour. The Brachyura is the largest and most specialized group of decapods. Though the Brachyura share similar design of the gastric mill teeth, there are distinct differences in the structures of medial tooth and lateral teeth among members of this infraorder (Patwardhan, 1935). These structures might have been modified to fit the needs of the animal. Natural selection seems to act on the morphology of the peripheral structures to optimize them for the diet of the species.

The development of the foregut and STNS has been examined in the lobster *Homarus gammarus* (Casasnovas and Meyrand, 1995). The final neuronal population in the STG occurs at early embryonic stages to create a single neural network. In contrast, the foregut itself develops slowly and it acquires all the specialized structures of the adult foregut during successive larval stages. During ontogeny, the single embryonic network is differentiated into the discrete neural networks that characterize the adult STNS, each having a specific neuronal population and a specific motor program and function (Selverston and Moulins, 1987; Harris-Warrick *et al*., 1992a). The STNS are more developmentally constrained by interdependence with structures of the foregut. Ancestral and developmental constraints may be imposed on the neural network to remain stable. Thus, the ontogenetic changes of the foregut structure and STNS appear to recapitulate the phylogenetic variability of them.

Neural networks and modulation

The multifunctional neural networks exist in the most primitive decapod species (Tazaki and Tazaki, 2000). Such neural networks exist even in the STG of the mantis shrimp *Squilla* (Tazaki and Chiba, 1994, 1995). Interactions among neurons in the STG of the shrimp *Penaeus* are particularly strong (Tazaki and Tazaki, 2000; Fig. 7 in this paper), compared to those in the crab *Cancer* where the DG neuron fires exclusively with the gastric pattern and the remaining neurons can switch back and forth to fire at different times in both the gastric and pyloric rhythms (Weimann *et al*., 1991). This fact is important for understanding how the stomatogastric motor system has evolved. Ontogenetic and phylogenetic evidences suggest that a common malacostracan ancestor may have possessed an original form of the neural network in which neurons are synaptically connected with each other to construct a single network.
Evolution of the motor system may follow two trends. One is to alter the number of muscles and to change the innervation pattern of muscles as previously described. The other is to alter the modulation of the neural networks. This is the most efficient way to evolve new outputs without disrupting structurally defined neural networks. As suggested by Katz (1991), types of configurations of the neural networks would have evolved to produce a wide range of motor patterns as the foregut structure has become complex. Alterations of both synaptic strength and intrinsic cellular properties in the presence of modulatory inputs can lead to changes in the neuronal constitution of the pattern generators as described in a variety of decapod species (Dickinson and Moulins, 1992).

The neuromodulatory inputs vary considerably between decapod infraorders. In particular, the transmitters used by the modulatory neurons and the responses of different target neurons to a single transmitter differ between infraorders (Katz and Tazaki, 1992). Evolution may act on both peripheral motor structures and neuromodulatory substances to produce new movements. Natural selection might act on a set of neuromodulators. The multifunctional neural networks in each of the taxa may be altered by selecting certain modulators from this set to create the output mediating behaviour appropriate to the motor structures as they have evolved to serve their functions.

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