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SELECTIVE RECRUITMENT OF INTERGANGLIONIC INTERNEURONES DURING DIFFERENT MOTOR PATTERNS IN *PLEUROBRANCHAEA*

BY CHRISTOPHER S. COHAN* AND GEORGE J. MPITSOS†

Department of Anatomy, Case Western Reserve University, Cleveland, Ohio 44106

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SUMMARY

The buccal and anterior head structures of the mollusc, *Pleurobranchaea*, participate in several types of behaviour which are generated largely by rhythmic activity produced in the brain and buccal ganglia. This paper examines the neuronal mechanisms (1) by which motor output from these ganglia is coordinated, and, (2) which underlie the generation of different motor patterns. Preliminary experiments indicated that the neuronal circuitry which produces the rhythms is contained in each of the paired buccal ganglia. The timing characteristics of the rhythms arise in the buccal ganglia and the pattern and symmetry of motor output in the brain roots are determined by activity in buccal cerebral interneurones (BCI) within the buccal ganglia.

Intracellular recordings showed that unique properties of individual cells within two pools of interganglionic interneurones, the BCI and paracerebral cells (PCC), determine in part the types of coordinated patterns that are produced. The BCI, which project to the brain, are a heterogeneous population of cells, based on: (1) the activity they evoke when they are depolarized; and (2) their activity patterns during rhythms that are evoked by buccal nerve stimulation. Evidence is presented to show that BCI are selectively recruited to produce the distinguishing features of different motor patterns. Similarly, the PCC were found to be a diverse group of cells that exert both excitatory and inhibitory effects on the nervous system. Stimulation of excitatory PCC in isolated nervous systems elicited a variety of activity patterns. These data suggest that the PCC may selectively recruit the BCI to produce different motor patterns and that differences in patterns can be attributed, in part, to the unique properties of individual cells within each pool of interneurones.

INTRODUCTION

Over the past 20 years the neuronal components which underlie discrete behavioural acts have been described in great detail, particularly in invertebrates

* Present address: Department of Zoology, University of Iowa, Iowa City, Iowa 52242.

† University of Oregon Health Science Center, Department of Medical Psychology, Portland, Oregon and Marine Sciences Center, Newport, Oregon.

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because of the experimental tractability of their nervous systems. Recent investigations have focused on the mechanisms by which neuronal components within a single nervous system could produce several different types of behavioural acts. On the one hand, individual cells within functional groups of neurones may be reserved for specific motor responses. For example, individual command fibres in crustaceans which control unique postures (Kennedy, Evoy, Dane & Hanawalt, 1967; Bowerman & Larimer, 1974) and swimmeret beating (Wiersma & Ikeda, 1964; Davis & Kennedy, 1972) have been identified. On the other hand, individual cells within functional groups may have multifunctional capabilities. These cells participate in several different motor responses. Some examples include command fibres in the cockroach which are used for both walking and flying (Ritzmann, Tobias & Fourtner, 1980) and command fibres in crayfish which produce several different postures (Atwood & Wiersma, 1967). Motoneurones with multifunctional properties have also been found (Wilson, 1962; Elsner, 1974). We have now found it possible to explore both mechanisms within a single preparation, the mollusc, *Pleurobranchaea*. The present paper focuses on the unique properties of interganglionic neurones which mediate specific motor responses in *Pleurobranchaea*. A subsequent paper (C. S. Cohan & G. J. Mpitsos, in preparation) will present evidence for multifunctional capabilities of neurones in this mollusc.

The anterior body structures of *Pleurobranchaea*, namely, the head, lips, mouth, jaws and buccal mass, participate in several types of behaviour. The differences in movement arise in part from differences in the phasing of rhythmic motor activity produced by the cerebropleural (brain) and buccal ganglia. In electrical recordings from isolated nervous systems two distinct motor patterns have been identified. One has been correlated with the active phase of regurgitation whereas the other has been assumed to represent feeding but may, in fact, be common to several other types of behaviour (e.g. the passive phase of regurgitation and rejection) (McClellan, 1982).

In the preceding paper (Cohan & Mpitsos, 1983) we demonstrated that patterns of rhythmic activity arise in an oscillatory locus within the buccal ganglion and are conveyed to the brain by the buccal-cerebral interneurones (BCI). Here, we shall examine how functional properties are dispersed among this pathway, as it drives and coordinates activity in the two ganglia. The BCI comprise a population of 20–30 neurones on each side of the buccal ganglion, have axons in the cerebrobuccal connectives (CBC) and are the only known direct connections from the buccal ganglion to the brain (Davis *et al.* 1974; Davis, Seigler & Mpitsos, 1973). The functional role and activity patterns of some of these cells have been studied previously (Kovac & Davis, 1977), but the manner by which this group of cells elicits and coordinates rhythmic activity in the brain has been unclear. We show here that the BCI are a heterogeneous population of cells which exhibit a variety of activity patterns and motor effects on the nervous system. These properties allow this group of cells to mediate changes in activity patterns of the brain which underlie the different types of behaviour produced by the anterior head structures. Similarly, a second group of interganglionic interneurones in the brain of *Pleurobranchaea* which have command properties (Gillette, Kovac & Davis, 1978), the paracerebral cells (PCC), will be shown to produce diverse motor effects when they are stimulated. Thus, these two pools of interneurones, the BCI and the PCC, each contain neurones which have

unique motor effects on the nervous system. This suggests that individual neurones within functionally related pools may be reserved for specific patterns of motor output in *Pleurobranchaea*.

MATERIALS AND METHODS

Preparations consisting of buccal, cerebropleural, pedal, visceral and stomatogastric ganglia were dissected from specimens of *Pleurobranchaea californica* which ranged in size from 100–300 ml body volume. These isolated preparations were pinned to the Sylgard (Corning) surface of a recording chamber and bathed in artificial sea water (Instant Ocean supplemented with 1 % dextrose) which was maintained at 11 °C by a circulating cooler.

Prior to electrophysiological recording the connective tissue sheaths which overlie the ganglia and which also surround the nerve trunks were removed. Recording techniques and criteria for identifying motor patterns were the same as those described in the preceding paper (Cohan & Mpitsos, 1983).

In addition, the following criteria were used to identify specific populations of neurones. The majority of BCI were located in the region of the buccal commissure as shown by back injections of cobalt. In each experiment, BCI that were penetrated with a microelectrode could be shown to evoke orthodromic action potentials in the CBC and, conversely, stimulation of the CBC produced antidromic action potentials in the soma. These potentials followed one for one at frequencies of 10 Hz. The PCC were identified by their antero-lateral location on the ventral surface of the brain in the region where the tentacle and small oral veil nerves exit. These cells also produced one for one orthodromic action potentials in the CBC and could be driven antidromically by CBC stimulation. Small oral veil (SOVN) and mouth nerve (MN) motoneurones were found on the ventral surface of the brain in the region anterior to the tract of fibres which exit to form the MN. These locations were confirmed by cobalt backfills of the SOVN and MN. Putative motoneurones which were penetrated during an experiment were activated both orthodromically and antidromically with respect to action potentials in their respective motor nerves.

RESULTS

Bilateral coordination of brain output

Both the buccal and brain ganglia are paired structures which are each joined by a commissure (cf. Fig. 1; Cohan & Mpitsos, 1983) through which axonal processes pass to the opposite side. In intact nervous systems, electrical stimulation of one medial gastro-oesophageal nerve (MGON) of the buccal ganglion produces bilaterally symmetrical motor output from the brain and buccal ganglia (Fig. 1A). After cutting the buccal commissure, however, little or no activity is produced in the brain and buccal ganglia that are contralateral to the side of stimulation, but, as before, the ipsilateral ganglia remain in-phase with one another (Fig. 1B). Stimulation of both MGON simultaneously in preparations where the commissure has been cut produces phase-locked activity in each pair of ipsilateral ganglia whereas the contralateral

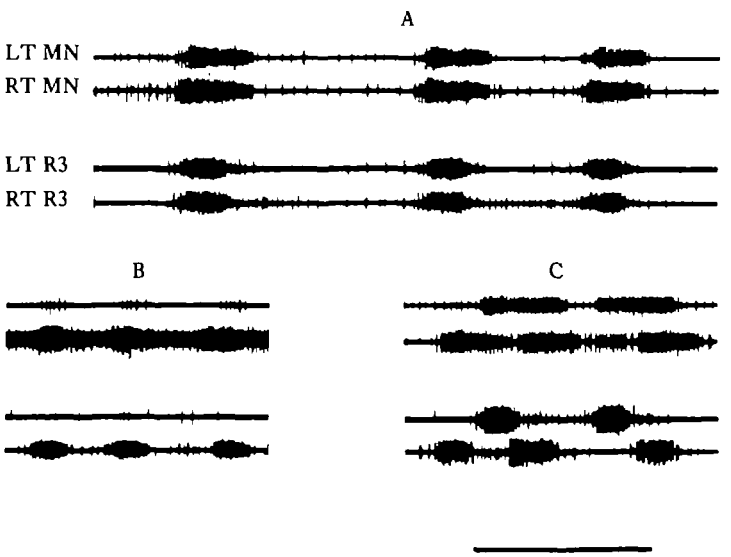

Fig. 1. Effect of cutting the buccal commissure on bilateral coordination. (A) Before the commissure is cut, MGON-evoked activity occurs approximately simultaneously in homologous roots of the ganglion. After cutting the commissure, (B) unilateral (right side) MGON stimulation elicits activity only weakly from the contralateral side of brain, whereas, (C) bilateral MGON stimulation causes activity in homologous roots of the brain and buccal ganglia to run out-of-phase. Notice in (B) that ipsilateral activity remains in-phase. Same preparation in (A), (B) and (C). ($N = 5$). Calibration: 20 s.

ganglia are not phase-locked (Fig. 1C). These findings show, first, that there is little, if any, drive within the brain itself that couples the paired brain ganglia. Second, each buccal ganglion contains the necessary circuit (or neurone) for driving the rhythmic activity in the ipsilateral motor nerves of the brain and buccal ganglia. And, third, bilaterally symmetric brain output depends on coordination between the paired buccal ganglia.

Unilateral coordination of brain activity may depend, in part, on mechanisms within the brain itself. Although most MN and SOVN motoneurones have single axonal processes in their respective nerves, some motoneurones were found to have processes in both these roots (Fig. 2A). These motoneurones fired rhythmically during the primary pattern (Fig. 2B). A survey of brain motoneurones, which fired in phase with the R3 activity of the buccal ganglion, revealed weak electrical coupling ($< 0{\cdot}10$) in about 11% of the pairs of neurones ($N = 64$) that were examined (unpublished observations). Such multiple projections of single motoneurones, and coupling between motoneurones might ensure that muscles which are innervated by different brain roots would contract in phase with one another.

Functional heterogeneity of the BCI

Coordination between the ipsilateral brain and buccal ganglia is thought to be accomplished by the action of the BCI since they are the only known inputs to the brain from the buccal ganglion. The manner by which this is accomplished was initially studied by using sucrose gap perfusions of the CBC (Cohan & Mpitsos, 1983).

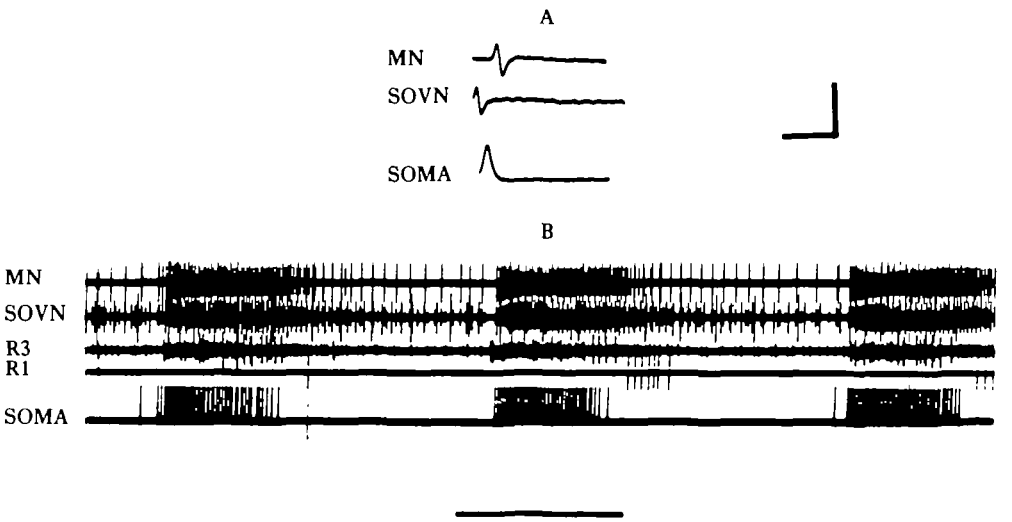

Fig. 2. Brain motoneurones with axons in two different roots. (A) Intracellular spike recorded in soma is correlated with extracellular spikes recorded in MN and SOVN. Antidromic stimulation of these nerves (not shown) produces a spike in the soma of motoneurones. (B) This motoneurone participates in the primary rhythm. ($N = 17$, 6 animals). Calibration: (A) 120 mV, 24 ms; (B) 10 s.

Solutions in which isotonic sucrose replaced most of the artificial sea water salts, suppressed or completely stopped conduction of activity in the CBC, whereas the addition of salts to this solution allowed for varying amounts of conduction to occur. In these and subsequent experiments, coordinated motor rhythms were activated by electrical stimulation of the MGON. In order to monitor the phase-locked activity in the two ganglia, recording electrodes were placed on R1 and R3 of the buccal ganglion and on the MN and SOVN of the brain. The amount of BCI activity that ascended to the brain beyond the block was monitored by an electrode on the CBC.

Normally, stimulation of the MGON evokes alternating activity in roots 1 and 3 of the buccal ganglia and rhythmic activity in the MN and SOVN of the brain which is phase-locked to buccal R3 activity (Fig. 3A). The application of low salt concentrations lowered the CBC activity to the extent that the brain output ceased altogether during rhythms that were evoked by MGON stimulation. At higher CBC activity, that resulted from higher salt concentrations, motor units of the MN and SOVN were selectively brought into phase-locked response with R3 activity (Fig. 3B). As different sucrose concentrations were applied, the output of one brain root was affected more than the other, which shows that the individual BCI units have differential effects on the populations of brain motoneurones. The records in Fig. 3 also support previous data (Kovac & Davis, 1977) that the BCI produce inhibition in the brain, since some of the motor units did not fire until after the cessation of bursts of activity in the BCI.

Paired intracellular recordings from BCI and putative brain motoneurones indicated that BCI have both excitatory and inhibitory effects on the brain. Some of the excitatory connections of the BCI appeared to be direct as shown by the one-to-one coupling of BCI spikes with postsynaptic potentials (psps) in the motoneurones which persisted at relatively high frequencies and had constant latencies (Cohan & Mpitsos, (1983).

These connections were specific in that penetrations of other SOVN and MN motor neurones failed to show inputs from these same BCI. Other excitatory and inhibitory connections which were found may be polysynaptic since the psps that were evoked by BCI stimulation were not always coupled in a one-to-one fashion. In some cases, connections were difficult to assess due to the lack of unitary psps in the motoneurones.

Intracellular characterization of BCI properties

Intracellular recordings demonstrated that individual BCI differ in at least two major respects, that is, the motor effects that they produce as a result of depolarization and the activity patterns that are evoked in them by tonic nerve stimulation (Table 1). Three distinct classes of cells could be differentiated. BCI class I cells (approximately 18%) produced motor output only in brain roots (MN or SOVN) when they were stimulated (for example, Figs 4A, 5A). This class consisted of two types of cells based on their activity patterns during different motor programmes. Class I-A cells were active during both the primary (Fig. 4B) and vomiting (Fig. 4C)

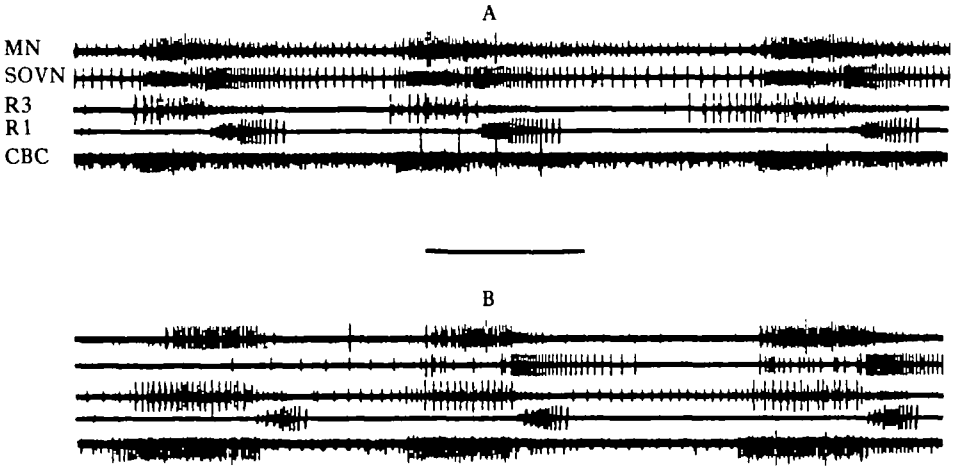

Fig. 3. Partial blockade of CBC activity using a sucrose gap. Activity that is evoked by MGON stimulation before (A) and after (B) block is applied. Notice in lower record the absence of SOVN activity during the first cycle of rhythm and the late appearance of SOVN activity after the CBC burst in the second cycle. ($N = 4$). Calibration: 10 s.

Table 1. *Classification of BCI*

BCI Class	Motor effect	Activity			
		Primary	Vom.	Primary and vom.	Non-modulated
I	Brain	—	3·7	14	—
II	Brain and buccal ganglion	2·8	0·9	4·7	—
III	No effect	2·8	—	12·1	58·9

Classification of BCI, based on the motor effects they evoked upon intracellular stimulation and the activity pattern they displayed when activity was evoked in the nervous system by stimulation of the MGON. Numbers represent percentages of cells. Motor effects were assayed by extracellular recordings from R3 and R1 of the buccal ganglion MN and SOVN of the brain. ($N = 107$, in 31 preparations.)

patterns. These cells were mostly active during the R3 phase of buccal activity in the primary pattern (Fig. 4B). They were found below the surface and at one consistently identifiable location (just anterior to the commissural tract and medial to the ventral white cell) on the ventral surface of the buccal ganglion. The class I-B cells, which were located below the ventral surface, also caused brain motor output when stimulated (Fig. 5A), but were active only during the vomiting motor pattern (Fig. 5C). In contrast to the former type, these cells were inhibited during R3 activity in the primary pattern (Fig. 5B) and became active during the R1 phase of buccal activity during vomiting (Fig. 5C).

The absence of activity during the primary pattern and the occurrence of activity during the vomiting pattern suggested that BCI class I-B neurones might mediate changes in brain activity which are known to occur during vomiting. In fact, when these cells were hyperpolarized during the vomiting motor pattern, the SOVN bursts which occurred in-phase with R1 were suppressed or eliminated from the pattern (Fig. 5C).

BCI class II cells (8 %) produced motor effects in the buccal ganglion as well as in the brain. These cells were located below the ventral surface of the ganglion and were consistently found to receive inhibitory input during the R3 burst of the primary pattern (Fig. 6A). Most of these cells, in turn, caused inhibition of R3 activity and excitation of R1 activity when they were depolarized during rhythms (Fig. 6B). In

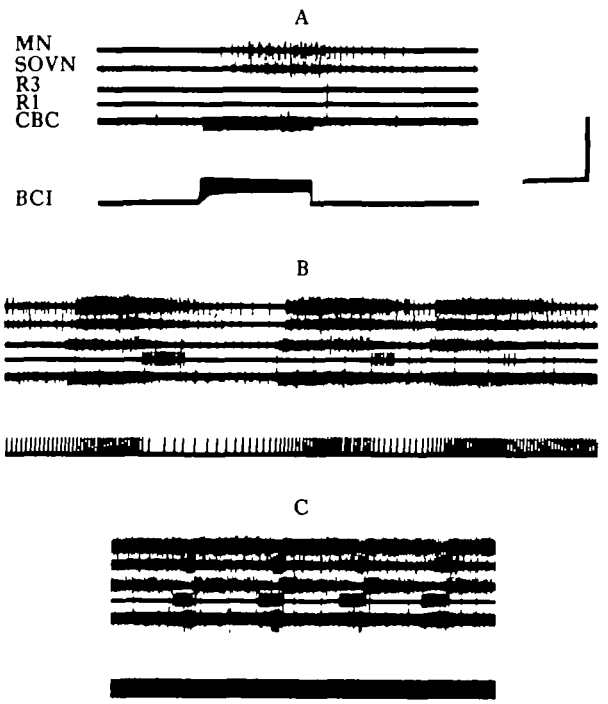

Fig. 4. BCI class I-A cell elicits activity in brain roots (A) when depolarized and is active during (B) the primary and (C) the vomiting motor patterns evoked by MGON stimulation. Same cell in (A), (B) and (C). Calibration: 200 mV, 8 s.

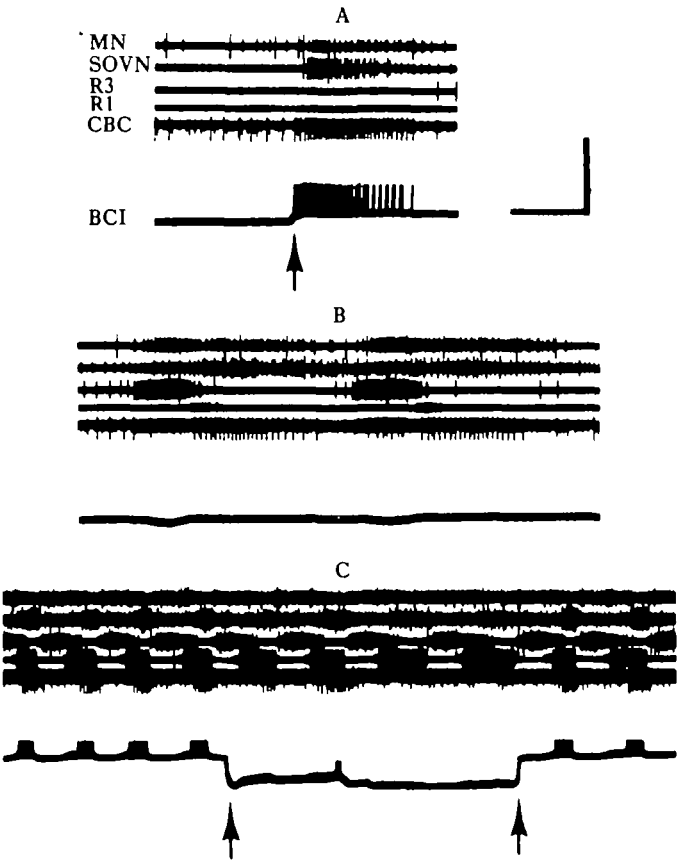

Fig. 5. BCI class I-B cell elicits activity in brain roots (A) when depolarized (arrow) but is phasically inhibited (B) during the R3 bursts of the primary pattern evoked by MGON stimulation. (C) During the vomiting motor pattern this BCI becomes active. Hyperpolarization of the cell (between arrows) during the vomiting pattern decreases or eliminates the SOVN bursts which occur in-phase with R1 activity. ($N = 3$ animals). Calibration: 160 mV, 8 s.

contrast, a few cells were found to inhibit R1 and excite R3 activity. These motor effects persisted after the CBC were severed, indicating that these effects are the result of local connections the BCI make in the buccal ganglion.

BCI class III cells, which comprised the majority of BCI that were sampled (74 %) did not produce motor effects in the buccal ganglion or the MN and SOVN of the brain. These cells were situated primarily on the ventral surface of the buccal ganglion in the region overlying the commissure. Most of these cells did not appear to receive synaptic inputs during motor patterns that were evoked by MGON stimulation and, consequently, they may be required for other types of motor patterns or they may serve as sensory interneurones. Some of these cells, however, were activated during MGON stimulation. Previous investigations have indicated that similar BCI inhibit interneurones (Gillette *et al.* 1978) and motoneurones (Kovac & Davis, 1977, 1980) in the brain of *Pleurobranchaea*. Among the cells which had no motor effects, but which received synaptic input were two giant BCI which were originally considered to have efference copy functions (Davis, *et al.* 1973, 1974). Experimentally induced

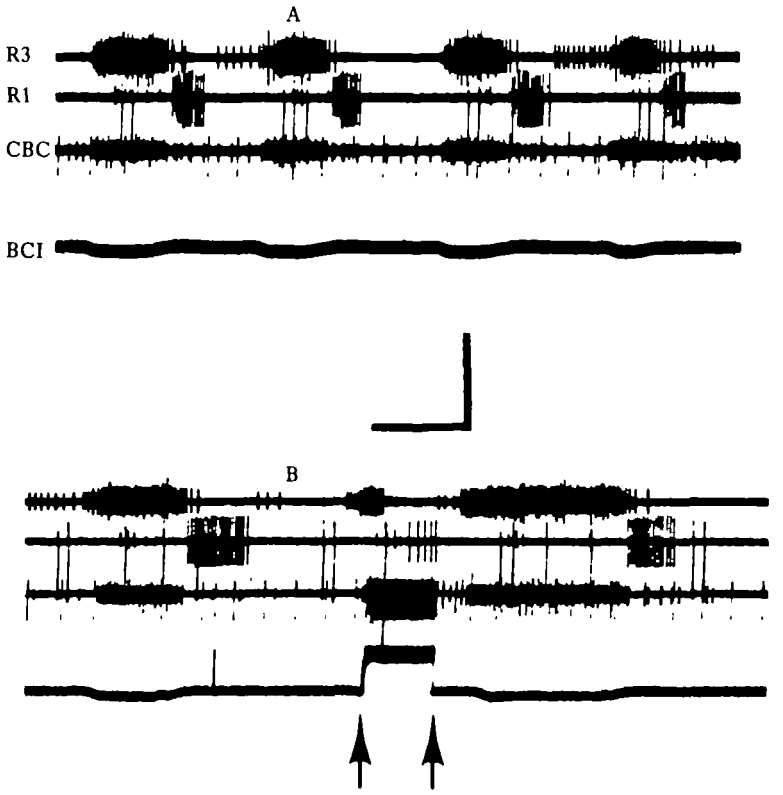

Fig. 6. BCI class II cell affects buccal motor output. (A) During the primary pattern this BCI receives inhibitory synaptic input in-phase with R3 activity. (B) Depolarization of this cell (between arrows) suppresses R3 activity and evokes some R1 activity. In this preparation the CBC were cut bilaterally. Calibration: 200 mV, 8 s.

alterations in the activity of these neurones, however, never changed the phasing or pattern of brain root activity relative to buccal output (Fig. 7). Inasmuch as the pattern for rhythmic activity in brain motoneurones is generated in the buccal ganglion (Cohan & Mpitsos, 1983) and since the giant BCI do not appear to mediate any overt responses in the brain, the role of the giant BCI in coordinating activity in the nervous system is presently unclear.

Brain inputs to BCI

Rhythmic motor patterns may be elicited in isolated nervous systems by electrical stimulation of the MGON (or stomatogastric nerve) and by tonic depolarization of individual neurones located in the buccal ganglion (ventral white cell, McClellan, 1980; Gillette, Gillette & Davis, 1980) and in the brain (paracerebral cells, Gillette *et al.* 1978). All these methods of stimulation evoke rhythmic motor patterns not only in the buccal ganglion, but also in the brain and, therefore, presumably must activate the BCI (Cohan & Mpitsos, 1983).

The paracerebral cells (PCC) are a small group of previously studied neurones (Gillette *et al.* 1978; Davis, 1977) which have been identified by their anterolateral

position on the ventral surface of the brain, and by the finding that stimulation of individual PCC causes rhythmic motor output from the nervous system of *Pleurobranchaea*. These cells were originally thought to be alike in their capacity to evoke motor output when they were depolarized, but more recent evidence has suggested that the PCC are heterogeneous in their motor effects (McClellan, 1980; Cohan, 1980). In the subsequent experiments the variability in motor effects produced by PCC stimulation will be examined.

Tonic depolarization of different PCC evokes a variety of motor patterns in the brain (Fig. 8). The variations in all cases are due to differences in the quantity and phasing of the brain output with respect to the buccal rhythm. Stimulation of some cells produces rhythmic activity in one brain root which is in-phase with R3 activity, while another brain root is more tonically activated (Fig. 8A). Other cells produce rhythmic activity in several brain roots which is in-phase with R1 activity (Fig. 8B). Still other PCC appear to drive activity in roots of the buccal ganglion without producing activity in the SOVN or MN of the brain (Fig. 8C). Such a variety of effects has been observed for PCC within a single animal as well as between animals. Our previous demonstration (Cohan & Mpitsos, 1983) that the PCC cannot evoke motor output by any local connections they may have in the brain, suggests that the variability in PCC excitatory effects is dependent on how these cells are connected to the functionally diverse population of BCI in the buccal ganglion. In this respect, Gillette *et al.* (1978) have shown that PCC can influence at least two different types of BCI. These interactions can be either excitatory or inhibitory and occur through polysynaptic pathways in the buccal ganglion.

In addition to their excitatory effects, it has previously been shown by McClellan (1980) that the PCC also exert an inhibitory influence on the nervous system. In support of these data we have found PCC which suppress brain output when they are depolarized during rhythms (Fig. 9). Although these inhibitory cells had their predominant effect in the brain, buccal activity was also affected. This suggests that

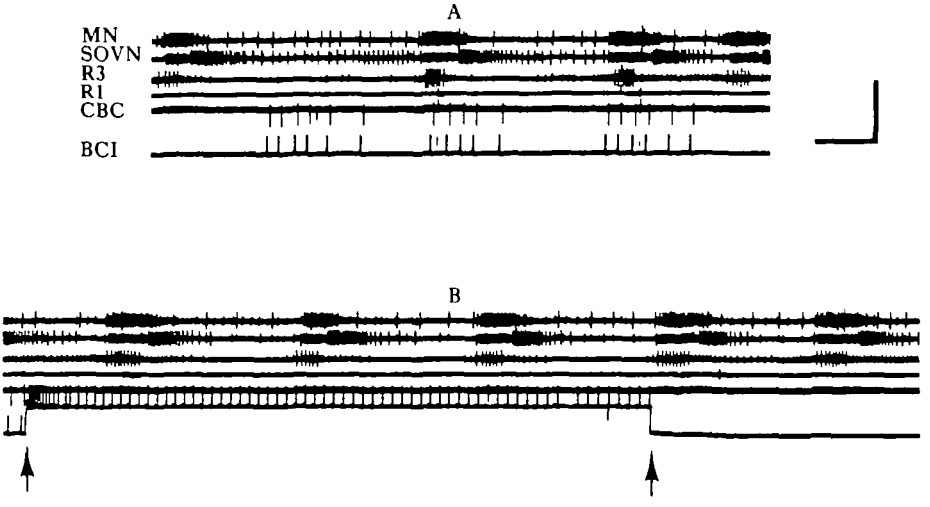

Fig. 7. Activity of the efference copy neurone during the primary pattern (A). (B) Depolarization of this cell (between arrows) does not alter the phasing of brain root activity relative to buccal output. Continuous records in A and B. ($N = 7$ animals). Calibration: 320 mV, 8 s.

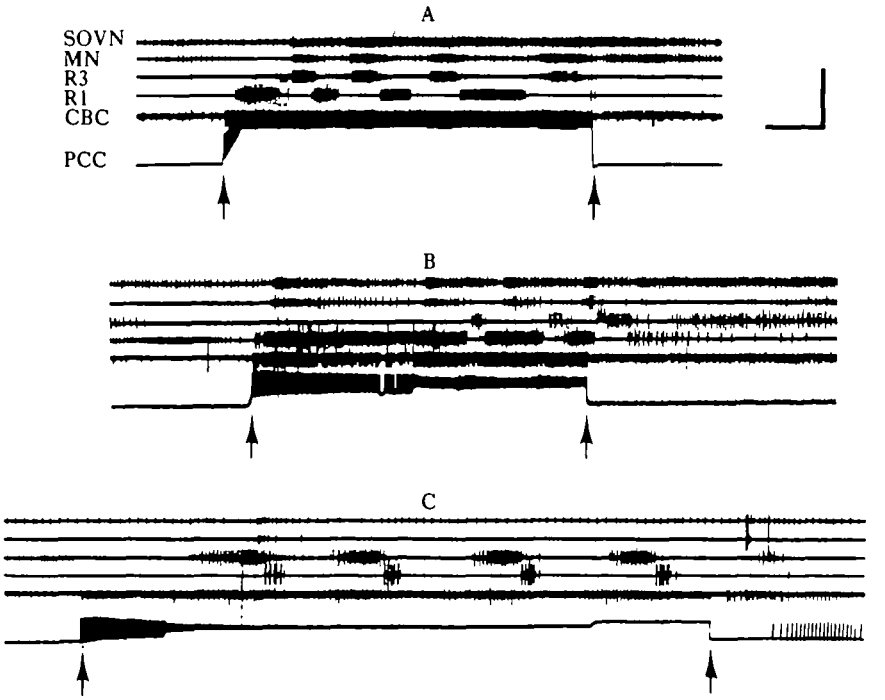

Fig. 8. Variation in excitatory effects of paracerebral cell stimulation. Depolarization of individual PCC produces rhythmic activity in SOVN and MN which is (A) in-phase with R3 activity in one preparation and (B) in-phase with R1 activity in another preparation. (C) Some paracerebral cells evoke rhythmic motor activity only from buccal roots. Calibration: (A), (C) 200 mV, (B) 240 mV; 8 s.

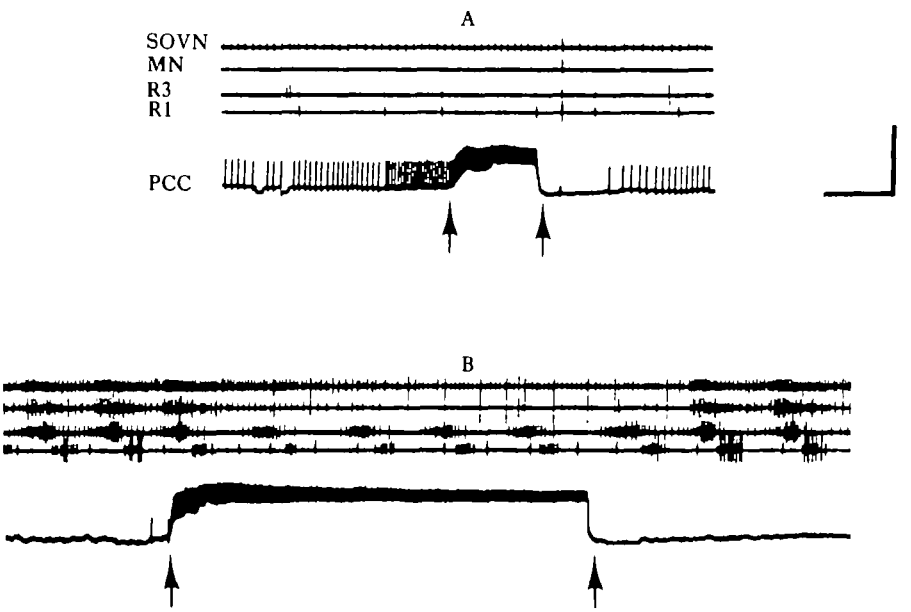

Fig. 9. Depolarization (between arrows) of inhibitory PCC produces (A) no effect in quiescent nervous system, but (B) inhibition, especially in brain roots, when depolarization occurs during rhythms. Same cell in (A) and (B). ($N = 5$, 6 animals). Calibration: 300 mV, 10 s.

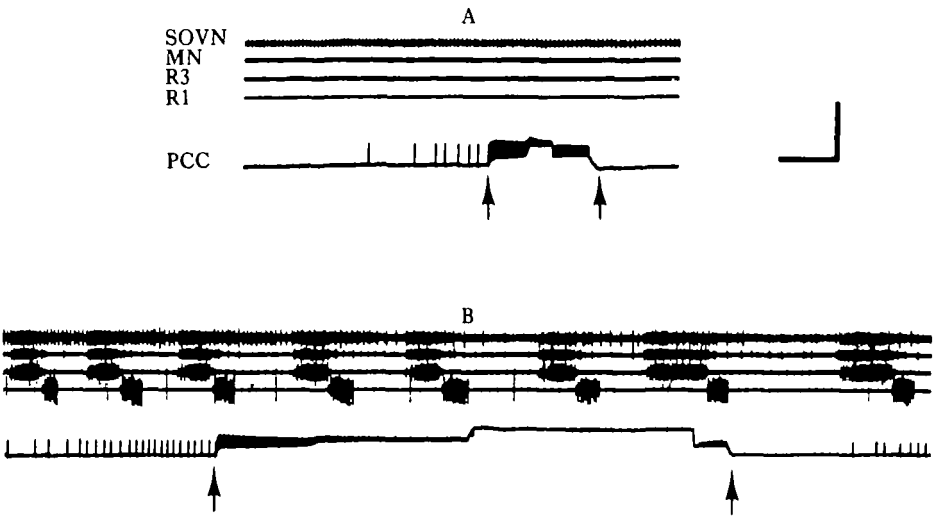

Fig. 10. Some PCC produce no noticeable motor effects when they are depolarized (between arrows) either (A) before or (B) during rhythms. ($N = 4$, 6 animals). Calibration: 160 mV, 8 s.

the PCC inhibition may be mediated by connections with BCI in the buccal ganglion, just as for the excitatory PCC. Occasionally, PCC were penetrated which did not produce any observable effects in the brain or buccal ganglia when they were stimulated (Fig. 10). The functional role of these cells is presently unclear.

DISCUSSION

A central question regarding the generation of behaviour is how common sets of neurones may be employed to produce a variety of motor responses. In the nervous system of *Pleurobranchaea*, a variety of motor patterns may be expressed by the action of intermediary neurones which selectively connect driving centres in the buccal ganglion with responding centres in the brain. These intermediary neurones, the BCI, are functionally heterogeneous, as shown by the differences among their responses and by the differences in the effects they produce on motoneurones. The response heterogeneity is characterized by the sign and timing of synaptic input to these cells during motor patterns that are evoked by tonic nerve stimulation. Whereas some cells receive excitatory synaptic input which is in phase with bursts of activity in R3 of the buccal ganglion, other cells are inhibited or do not appear to receive any input. Furthermore, this variation in synaptic input causes some BCI to respond with action potentials in only one motor pattern, whereas other BCI produce action potentials in two patterns. The heterogeneity of BCI effect is characterized by the sign and distribution of their influence on motoneurone populations. Some cells inhibit (Kovac & Davis, 1977, 1980) or excite motoneurones in the brain, whereas others affect buccal motor output. Thus, the BCI are a functionally diverse group of cells which participate in the generation of multiple motor programmes.

The functional diversity of the BCI raises the question of how coordinated motor output is produced by these cells. Preparations in which the buccal commissure had

been severed indicate that there is very little driving activity between the paired cerebral ganglia for producing brain motor output (Fig. 1). The coordination of motor output from the nervous system of *Pleurobranchaea*, therefore, must depend primarily on circuits in the buccal ganglion which are responsible for generating the rhythmic motor patterns. These circuits must provide the input to the BCI for driving and coordinating the ipsilateral brain root activity. Moreover, buccal circuits must also be responsible for the coactivation of functionally similar BCI in the paired buccal ganglia in order to produce the bilaterally coordinated activity in the brain.

Although functionally similar BCI are necessary for the generation of coordinated activity within a motor pattern, heterogeneity in the BCI population provides the means for the generation of different motor patterns. The variations in motor patterns which underlie different types of behaviour in *Pleurobranchaea* are the result of differences in motor output of both the brain and buccal ganglia (McClellan, 1982). Some of the higher order cells in the buccal ganglion which are responsible for producing these changes have already been studied (McClellan, 1980). Differences in motor output from the brain consist of an increase in tonic firing and a shift in the phasing of rhythmic activity (cf. Fig. 5A) which signals the transition from the primary to the vomiting motor pattern. In the preceding paper (Cohan & Mpitsos, 1983) we demonstrated that all of the motor patterns that are generated in isolated nervous systems must utilize the BCI to drive and coordinate the brain output, whether these patterns are initiated by buccal or brain stimulation. Therefore, the variations in brain output must be attributable to changes in the activity of the BCI.

Intracellular recordings have shown that differences in motor output of the brain result from (1) the selective activation of particular BCI which bring in units and features that are unique to a pattern, and (2) changes in the activity of BCI that participate in several motor patterns. Thus, heterogeneity of the BCI pool provides the source for variations in motor output patterns of the brain in isolated nervous systems. Insofar as the only direct connection between the brain and buccal ganglia are the two bilaterally paired CBC, which contain the axons of the BCI, it seems reasonable to postulate that the BCI play an equally important role in driving and coordinating motor patterns in intact animals.

The heterogeneity of action of the BCI goes beyond their intermediary role of supplying the drive and pattern of activity to brain motoneurones for the production of different motor patterns. The BCI are also involved in the modification of brain motor output that they themselves do not produce (Kovac & Davis, 1977, 1980). As we have shown here, they can also affect motor activity in the buccal ganglion. The BCI are not only activated by the PCC but they also feed back onto the PCC (Gillette *et al.* 1978) and, therefore, modify their own inputs. The finding that some BCI do not receive synaptic input during rhythms that are evoked in isolated nervous systems suggests the possibility that these neurones may mediate additional responses as yet unknown.

The BCI are activated by cells in the brain as well as by cells in the buccal ganglion. The paracerebral cells which are located in the brain of *Pleurobranchaea* evoke rhythmic motor output from the nervous system when they are depolarized (Gillette *et al.* 1978). Previously, we showed that the PCC evoke motor output from the brain by first activating the BCI in the buccal ganglion (Cohan & Mpitsos, 1983). In the

present study it was shown that the PCC are a heterogeneous population of cells which exert a variety of motor effects on the nervous system. These findings indicate that the PCC can selectively influence the BCI in addition to activating the buccal oscillator.

Some of the PCC clearly have the ability to initiate activity when they are stimulated and thus appear to have command properties. The fact that these cells display a variety of excitatory effects, however, suggests that the PCC may participate in several motor patterns or, alternatively, they may be used in combination for individual patterns (see also Atwood & Wiersma, 1967; Bowerman & Larimer, 1974; Davis & Kennedy, 1972; McClellan, 1980). This latter possibility is further supported by the finding of inhibitory PCC which can selectively suppress on-going activity in the nervous system (McClellan, 1980). Thus, the property of command may be dispersed among this population of cells. Furthermore, since the PCC can selectively call into play different BCI they may share the role of coordination in addition to their command roles. These properties which allow functional roles to be dispersed among cells and shared between groups of cells may be the means by which a limited number of neurones could be used to generate a variety of motor patterns.

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