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NEURAL MECHANISMS OF MOTOR PROGRAM SWITCHING IN THE MOLLUSC *PLEUROBRANCHAEA*

I. Central Motor Programs Underlying Ingestion, Egestion, and the "Neutral" Rhythm(s)[1]

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Abstract

The buccal musculature of the carnivorous gastropod *Pleurobranchaea* is used in three cyclic patterns of coordination underlying, respectively, ingestion, egestion, and a third, unknown behavior(s) (Croll, R. P., and W. J. Davis (1981) J. Comp. Physiol. *145:* 277–287; Croll, R. P., and W. J. Davis (1982) J. Comp. Physiol. *147:* 143–154). The corresponding three motor programs can be identified and distinguished in the intact animal (Croll, R. P., and W. J. Davis (1981) J. Comp. Physiol. *145:* 277–287), the reduced preparation (Croll, R. P., and W. J. Davis (1982) J. Comp. Physiol. *147:* 143–154, and the present paper), and the isolated CNS (present paper), on the basis of several qualitative and quantitative criteria. Distinguishing parameters developed here include: (*1*) the activity of the salivary duct, which bursts in phase with protraction during ingestion, is silent during egestion, and usually bursts biphasically and in antiphase with protraction during the third ("neutral") rhythm(s); and (*2*) the protractor duty cycle, which is generally 33 to 50% during ingestion, >50% during egestion, and <33% during the neutral rhythm(s). Retractor duty cycles did not differ significantly between the three motor programs. The neutral rhythm(s) may be a low-intensity version of the ingestion motor program, with which it shares most features. The three buccal motor programs can be elicited in the reduced preparation (sensory feedback intact) and in the isolated, deafferented CNS. Therefore, multiple motor programs in this metastable motor system are each endogenous to the CNS; i.e., they can each be generated by a central pattern generator(s) in the absence of sensory feedback. Deafferentation does, however, increase the retractor duty cycle, suggesting that sensory feedback normally terminates retractor bursts. Comparisons between these results and those of McClellan (McClellan, A. D. (1982) J. Exp. Biol. *98:* 195–211, 213–228) on the same motor system are discussed.

Animals normally perform more than one behavior using the same muscles and motoneurons. The operation of the same motor units in different patterns of coordination (motor programs) mediating different behaviors has been described as "metastable coordination" (Ayers and Davis, 1977). The selection of a particular stable coordination pattern in a metastable motor system has been termed motor program switching (Croll and Davis, 1981, 1982). By means of motor program switching, organisms achieve a greater behavioral repertory within the constraints imposed by a fixed endowment of neurons and muscles.

Examples of motor program switching have been documented at several levels in the animal kingdom, including gastropod molluscs (e.g., Kupfermann, 1974), crustaceans (e.g., Wyse and Dwyer, 1973; Pasztor and Clarac, 1983), locusts (e.g., Wilson, 1962; Hoyle, 1964; Elsner, 1974; Pflüger and Burroughs, 1978a, b; Pearson, 1983), amphibians (Kahn and Roberts, 1982; Kahn et al., 1982), dogs (e.g., Sherrington, 1906), cats (e.g., Miller et al., 1975a, b; Halbertsma, 1983), and humans (e.g., Thorstensson et al., 1982). However, despite the generality of the phenomenon, the neural mechanisms underlying motor program switching have not been determined. Indeed, little evidence is available on whether multiple motor programs underlying discrete behaviors in the same motor systems are all endogenous to the central nervous system (CNS), i.e., whether they are each centrally programmed and can therefore be generated in the absence of sensory feedback from the respective movements.

The present series of papers is a continuation of previous work employing a simple "model" system, the gastropod mollusc *Pleurobranchaea*, to study the neural basis of motor program switching. Intact *Pleurobranchaea* show three discrete buccal motor programs: one associated with ingestion, a second associated with egestion, and a slow third rhythm that has no

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known behavioral function (Croll and Davis, 1981). These same motor programs can be identified in the reduced preparation, consisting of the buccal mass and attached CNS (Croll and Davis, 1982). In the present work we show that all three motor programs can also be elicited and distinguished in the isolated CNS preparation. It is well established that many motor programs are endogenous to the CNS; i.e., they can be generated by purely central mechanisms (for reviews see Grillner, 1975, 1981; Kennedy and Davis, 1977; Delcomyn, 1980). The present study extends the conclusion to multiple motor programs in a metastable motor system. The present work also develops quantitative criteria for distinguishing the three buccal motor programs, as required for the second and third papers of this series (Croll et al., 1985a, b).

Materials and Methods

General Methods

Specimens of *Pleurobranchaea californica* were obtained by trawling in Monterey Bay at depths of 60 to 90 m using the University of California at Santa Cruz research vessel *Scammon*. Prior to experiments animals were maintained in fresh, running sea water at ambient temperatures (11 to 17°C) at the University of California at Santa Cruz's Long Marine Laboratories and were fed fresh, raw squid weekly. Animals used for experiments were 100 to 600 ml in volume.

Preparations

The whole animal preparation. To study the behavioral effects of stimulating the stomatogastric nerve (SGN) in the whole animal, specimens were partially anesthetized by cooling them to 4°C for 30 min. The animal was then pinned in a dissecting tray under sea water, and a small anterior dorsal incision was made above the esophagus. The esophagus was drawn out of the body through the incision, and the SGN was dissected free and drawn into a polyethylene suction electrode for stimulation while the behavioral effects were observed visually. Behavioral observations were made only after specimens were gradually returned to 11 to 17°C.

The reduced preparation. The reduced preparation consisted of the surgically isolated buccal mass and the overlying brain (cerebropleural ganglion) and buccal ganglion, as fully described in previous publications (e.g., Croll and Davis, 1982).

The isolated CNS preparation. The isolated CNS preparation consisted of the brain and buccal ganglion, connected by the paired cerebrobuccal connectives (CBCs), all of which were glued (Super Glue; Duro Corp.) to the Sylgard (Dow Chemical) bottom of a temperature-controlled (14 ± 1°C) experimental chamber under sea water. In some experiments the salivary duct (SD) was left attached to the salivary nerve (SN), whereas in others, the SD was removed and extracellular recordings were made directly from the SN. In the latter case the activity of the "fast burster" unit in the SN was taken as an index of SD activity, since the primary SD muscle potentials occurred 1:1 with action potentials in the fast burster unit (not shown), as seen also in *Limax* (Prior and Gelperin, 1977; Reingold and Gelperin, 1980; Prior and Grega, 1982).

Electrophysiological methods

Extracellular recordings from nerves and muscles were obtained using polyethylene suction electrodes. Muscles included in this study are identified in Davis et al. (1973) and confirmed in Croll and Davis (1981). Specific muscles from which electromyograms were made are described under "Results." All electrophysiological recordings were amplified and displayed simultaneously on a Tektronix oscilloscope and a Gould-Brush eight-channel pen recorder for making permanent records.

Elicitation of motor programs

Previous studies on the reduced preparation showed that CBC stimulation causes the ingestion motor program and no other buccal motor program (Croll and Davis, 1982). The motor program for ingestion was therefore induced here by extracellular stimulation of the CBC(s). Rectangular pulses, 1 msec in duration, were delivered at 1 to 20 Hz and 5 to 10 V. In the reduced preparation ingestion was identified behaviorally by monitoring the inward movement of a plastic worm (no chemosensory stimuli present) placed into the buccal cavity, using a position transducer attached to the worm (Sandeman, 1968), as previously reported (Croll and Davis, 1982).

The motor program for egestion was generally induced by relatively high voltage (approximately double the threshold voltage for cyclic motor output, i.e., ~ 15 V and higher) extracellular stimulation of one or both SGNs using 1-msec pulses delivered at 0.5 to 2 Hz. On occasion, the egestion motor program occurred during lower voltage SGN stimulation. In the reduced preparation egestion movements were also confirmed behaviorally by monitoring the outward movement of a plastic worm with a position transducer.

The neutral motor program(s) was generally elicited by low voltage (usually ~10% above the threshold voltage for cyclic motor output, i.e., ~5 to 10 V) extracellular stimulation of the SGN(s) using 1-msec pulses delivered at 0.5 to 2 Hz. In addition, the neutral rhythm(s) often occurred spontaneously. In the intact animal the frequent occurrence of this motor program is not accompanied by a clearly defined behavior and, hence, the behavioral significance of this motor program is unknown.

Data analysis and interpretation

Parameters of muscle activity measured from pen recordings included: (*1*) the frequency of the motor rhythm, defined as the reciprocal of the interburst interval and expressed in hertz; (*2*) the protractor duty cycle, defined as the duration of the major burst of protractor activity (m 4 in the reduced preparation, buccal nerve root 1 (r 1) in the isolated CNS), divided by the period of the corresponding motor output cycle; and (*3*) the retractor duty cycle, defined as the duration of the major burst of retractor activity (m 3 in the reduced preparation, buccal nerve root 3 (r 3) in the isolated CNS), divided by the period of the corresponding motor output cycle. Buccal r 1 and r 3 innervate, respectively, protractor and retractor muscles (Davis et al., 1973; Croll and Davis, 1982). These parameters were computed for episodes of the ingestion motor program, the egestion motor program, and the neutral rhythm(s), each lasting from 3 to 12, complete, contiguous cycles of motor output. Results are expressed as means calculated from individual episodes of the respective motor programs (Figs. 2, 4, and 6) or means of these means (Table I).

Statistical analyses were performed on the mean values of individual means (Table I) using nonparametric (Mann-Whitney *U* test) procedures. Unless otherwise stated, all probability levels given refer to the Mann-Whitney *U* test. The $p < 0.05$ level was used as the criterion for significant differences, although most probability levels were substantially lower, as reported under "Results." The nature of the hypothesis to be tested dictated the use of one-tailed or two-tailed tests. One-tailed tests were used whenever previous studies gave reason to make a directional *a priori* hypothesis, while two-tailed tests were used in the absence of a directional *a priori* hypothesis. Unless otherwise indicated the probability levels reported refer to two-tailed tests.

Results

The identity of a motor program as corresponding to a particular behavior of course requires a preparation sufficiently intact to exhibit recognizable behavior. Our approach, therefore, has been to compare the motor programs elicited by specific types of electrical stimuli in the reduced preparation, where the movement of objects through the buccal mass can be monitored, with motor programs elicited by the same type of stimuli in the isolated CNS preparation. This procedure was followed for each of the three discrete buccal motor programs identified previously by electromyography in intact, behaving specimens (Croll and Davis, 1981).

The ingestion motor program

Previous work showed that tonic extracellular stimulation of the CBCs causes ingestion of objects placed into the buccal cavity of the reduced preparation and never causes egestion (Croll and Davis, 1982). Accompanying ingestion is a characteristic pattern of muscle activity, in which retractor m 3 and protractor m 4 alternate bursts, and the SD (or SN) discharges bursts in phase with protraction (see Fig. 10 in Croll and Davis, 1982). These results were repeatedly confirmed here.

In the isolated CNS preparation studied here, a similar pattern of motor activity is elicited by tonic CBC stimulation (Fig. 1). Quantitative comparison of this motor program with the ingestion motor program elicited in reduced preparations (Fig. 2, Table I) showed that most parameters measured were not significantly different, including the mean frequencies of the rhythm ($p > 0.15$), the protractor duty cycle ($p > 0.23$), and the retractor duty cycle ($p > 0.43$).

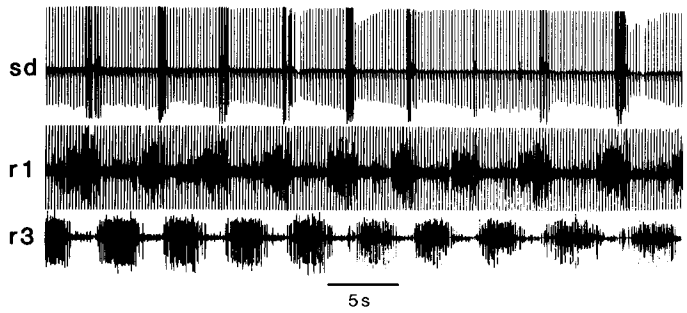

Figure 1. The ingestion motor program elicited by tonic extracellular stimulation of the CBCs (stimulus artifacts visible in the interburst periods) in the isolated CNS. *sd*, muscle potentials recorded from the salivary duct; *r1* and *r3*, extracellular recordings, respectively, from buccal nerve root 1, which normally innervates radula protractor muscles, and buccal nerve root 3, which normally innervates radula protractor muscles.

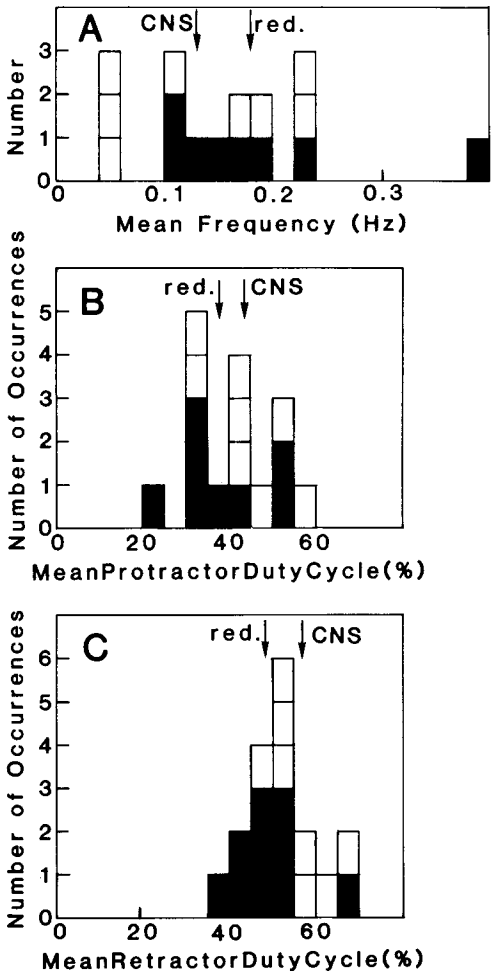

Figure 2. Histograms of mean values of the frequency (*A*), protractor duty cycle (*B*), and retractor duty cycle (*C*) for several episodes of the ingestion motor program in the reduced preparation (*solid blocks*) and the isolated CNS (*open blocks*). *Downward arrows* near the *top* of each histogram show the means for the reduced preparation (*red*) and isolated central nervous system (*CNS*).

The egestion motor program

Previous work showed that tonic, high voltage stimulation of the SGNs causes egestion of objects placed into the buccal cavity and never causes ingestion (Croll and Davis, 1982). Accompanying egestion is a characteristic pattern of muscle activity, in which protractor and retractor muscles alternate bursts, but protractor discharge is more intense. In addition, SD activity is suppressed, as is buccal constrictor m 5 discharge (Fig. 11*B* in Croll and Davis, 1982). These findings were repeatedly confirmed here.

In the isolated CNS preparation studied here, a similar pattern of motor activity is elicited by the same nerve stimulus (Fig. 3). Quantitative comparison of this motor program with the egestion motor program (Fig. 4, Table I) showed that the two motor programs were indistinguishable with regard to mean frequency ($p > 0.26$) and mean protractor duty cycle ($p > 0.77$). The mean retractor duty cycle was greater in the isolated CNS ($p \leq 0.029$), consistent with Siegler's (1977) finding that sensory feedback associated with protraction terminates retractor discharge (see "Discussion").

The neutral rhythm(s)

Previous work showed that tonic, low voltage stimulation of the SGN(s) causes a comparatively low frequency buccal rhythm with no accompanying net movement in either direction of objects placed into the buccal cavity (Croll and Davis, 1982). The accompanying motor program is qualitatively similar to the ingestion motor program, except that the SD fires either monophasically before the main protractor burst or, more typically, biphasically, with a small burst of activity occurring before and after (or slightly overlapping) the principal retractor discharge (Fig. 11*A* in Croll and Davis, 1982). These results were repeatedly confirmed here.

In the isolated CNS preparation studied here, a similar pattern of motor activity is elicited by the same nerve stimulus (Fig. 5). Quantitative comparison of this motor program with the neutral rhythm(s) (Fig. 6, Table I) showed that the two motor programs were indistinguishable with regard to mean frequency ($p > 0.2$) and mean protractor duty cycle ($p > 0.2$). The mean retractor duty cycle was greater in the isolated CNS ($p \leq 0.002$), as in the case of the egestion motor program described above, supporting a role for sensory feedback in shaping retractor discharge. The mean retractor duty cycle exceeded the mean protractor duty cycle ($p \leq 0.001$), as found for the neutral rhythm(s) in the reduced preparation (Croll and Davis, 1982) and whole animal (Croll and Davis, 1981).

Comparisons between different buccal motor programs

The foregoing parameters characterize each motor program but do not distinguish between them. Toward this end we quantitatively compared the parameters of each motor program to those of the other two.

Ingestion versus egestion. Mean frequencies were not significantly different ($p > 0.45$), as found also in the reduced preparation ($p > 0.83$). The mean protractor duty cycles differed in the reduced preparation ($p \leq 0.001$) and in the isolated CNS ($p \leq 0.001$). In contrast, retractor duty cycles were not significantly different in the reduced preparation ($p > 0.86$) or in the isolated CNS ($p > 0.56$). A protractor duty cycle criterion of 50% enabled correct distinction between the ingestion and egestion motor programs (each identified by other criteria, including direction of movement of the plastic worm placed in the buccal cavity and SD or SN activity) in 13 of 15 (87%) reduced preparations and 15 of 17 (88%) isolated CNS preparations.

TABLE I

Means and standard deviations of mean quantitative parameters of motor output programs in the reduced preparation and in the isolated CNS of Pleurobranchaea

Protraction duty cycles were calculated from protractor m 4 discharge (reduced preparation) or from protractor nerve (buccal root 1) discharge (isolated CNS). Retractor duty cycles were calculated from retractor m 3 discharge (reduced preparation) or from retractor nerve (buccal root 3) discharge (isolated CNS).

Motor Program	Type of Preparation	Sample Size		Mean Frequency (Hz)	Mean Protraction Duty Cycle (%)	Mean Retraction Duty Cycle (%)
		Episodes	Preparation			
Ingestion	Reduced	8	8	0.18 (0.9)[a]	37.8 (10.1)	48.6 (9.2)
	Isolated CNS	8	7	0.13 (0.08)	44.1 (8.2)	56.9 (6.7)
Egestion	Reduced	7	6	0.17 (0.05)	65.0 (11.7)	47.7 (10.5)
	Isolated CNS	9	6	0.16 (0.04)	66.8 (11.2)	54.3 (9.5)
Neutral rhythm(s)	Reduced	9	7	0.10 (0.07)	22.6 (15.4)	29.6 (11.0)
	Isolated CNS	19	14	0.11 (0.05)	18.5 (7.3)	52.2 (11.6)

[a] Numbers in parentheses, standard deviations.

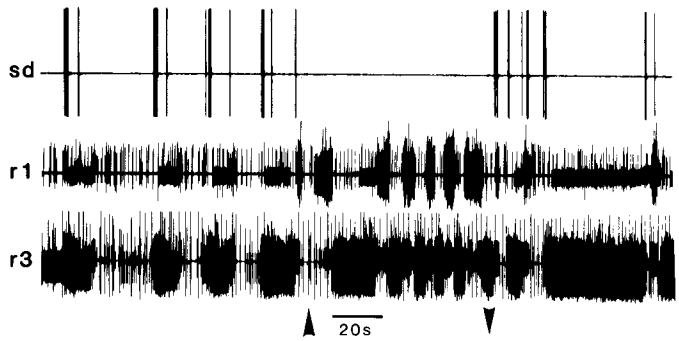

Figure 3. The egestion motor program in the isolated CNS, which occurred, in this case, spontaneously (between *arrowheads*). *sd*, muscle potentials from the salivary duct; *r1* and *r3*, extracellular recordings from the buccal protractor and retractor nerve, respectively.

Neutral rhythm(s) versus ingestion. Mean frequencies were significantly different in the reduced preparation ($p \leq 0.5$) but not the isolated CNS ($p > 0.2$). The mean protractor duty cycles differed in the reduced preparation ($p \leq 0.05$) and the isolated CNS ($p \leq 0.002$). The mean retractor duty cycles differed in the reduced preparation ($p \leq 0.01$) but not in the isolated CNS ($p > 0.2$). A protractor duty cycle criterion of 33% enabled correct distinction between the two motor programs (each identified by other criteria) in 12 of 17 (71%) reduced preparations and 26 of 27 (96%) isolated CNS preparations.

Neutral rhythm(s) versus egestion. Mean frequencies were not significantly different in the reduced preparation ($p > 0.05$) but were in the isolated CNS ($p \leq 0.01$). The mean protractor duty cycles were different in both the reduced preparation ($p \leq 0.002$) and the isolated CNS ($p \leq 0.002$). Retractor duty cycles were not significantly different in either preparation ($p > 0.2$). A protractor duty cycle criterion of 33% enabled correct distinction between the neutral and egestion motor programs (each identified by other criteria) in 81% of 16 reduced preparations and 100% of 27 isolated CNS preparations.

Role of the stomatogastric nerve

We studied the role of this nerve because of conflicting claims regarding the effects of its stimulation (cf. Davis et al., 1973, and McClellan, 1982a, b; see "Discussion"). In 50 whole animal preparations, SGN stimulation usually caused rhythmic buccal movements. Ingestion was seen in only two preparations, and egestion was never observed even at high intensities of stimulation. In 30 reduced preparations, low voltage SGN stimulation also caused rhythmic buccal movements, but ingestion was

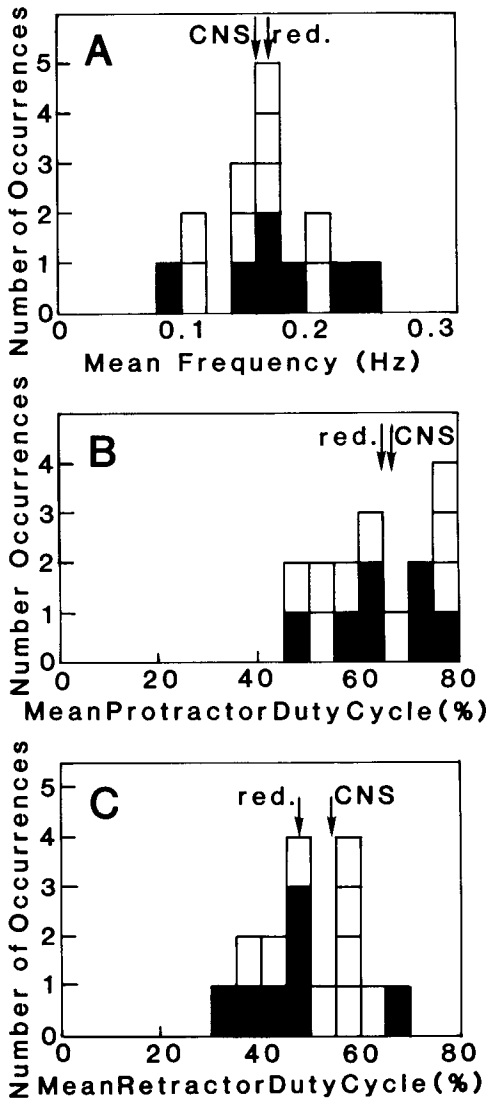

Figure 4. Histograms of mean values of the frequency (*A*), protractor duty cycle (*B*) and retractor duty cycle (*C*) for several episodes of the egestion motor program in the reduced preparation (*solid blocks*) and the isolated CNS (*open blocks*). *Downward arrows* near the *top* of each histogram show the mean of means for the reduced preparation (*red*) and isolated central nervous system (*CNS*).

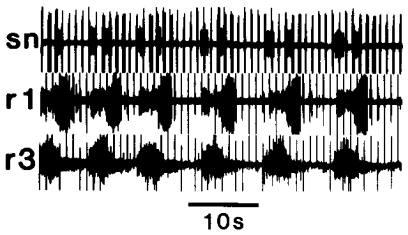

Figure 5. The neutral rhythm(s) elicited by tonic extracellular stimulation of the SGN at low stimulus intensities (stimulus artifacts visible on *upper trace*) in the isolated CNS. *sn*, extracellular activity recorded from the salivary nerve; *r1* and *r3*, extracellular recordings from buccal protractor nerve root 1 and buccal retractor nerve root 3.

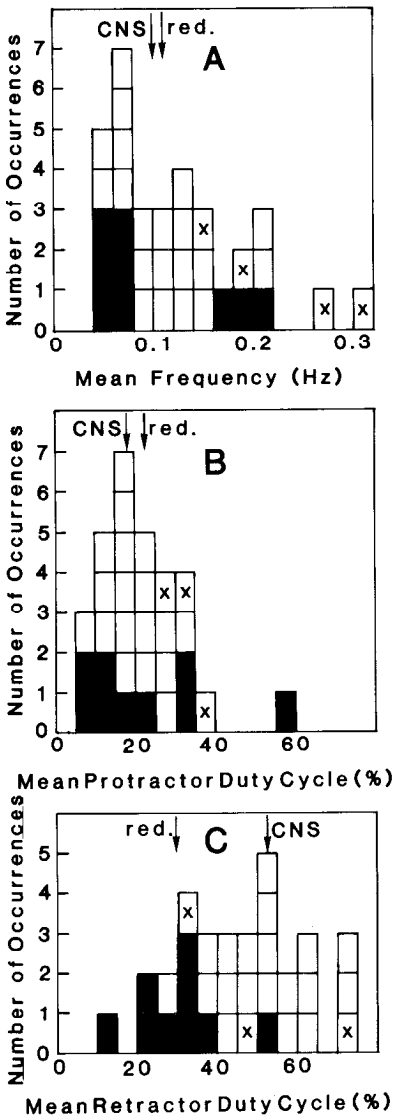

Figure 6. Histograms of mean values of the frequency (*A*), protractor duty cycle (*B*), and retractor duty cycle (*C*) for several episodes of the neutral rhythm(s) in the reduced preparation (*solid blocks*) and the isolated CNS (*open blocks*). *Downward arrows* near the *top* of each histogram show the mean of means for the reduced preparation (*red*) and isolated central nervous system (*CNS*). *Symbols* with *X*'s indicate episodes in which SD discharge was monophasic and concurrent with protractor activity, characteristic of the ingestion motor program.

found in one preparation only. At higher intensities of stimulation, egestion bouts reliably resulted, preceded and followed by a buccal rhythm that caused no net movement of the squid, analogous to previously published motor output patterns (Croll and Davis, 1982, Fig. 11*B*).

In an independent series of experiments motor output was recorded during SGN stimulation and quantitatively analyzed in both the reduced preparation and the isolated CNS. Protractor duty cycle increased with the frequency of the motor rhythm in the reduced preparation ($r = +0.93$) and in the isolated CNS ($r = +0.46$) (Fig. 7). Both correlation coefficients are significantly different from zero (t tests, $p \leq 0.001$ and $p \leq 0.05$, respectively). The respective slopes were 209 and 273, significantly different from zero (t tests, $p \leq 0.001$ and $p \leq 0.05$, respectively) and from each other (analysis of covariance, $F = 7.6$, $p \leq 0.001$). The protractor duty cycle over this range of frequencies varied continuously, from values characteristic of the neutral rhythm(s) (<33%) to values characteristic of the ingestion motor program (33 to 50%) but seldom reached values characteristic of the egestion motor program (>50%) (Fig. 7).

In these same experiments the retractor duty cycle (Fig. 8) likewise increased with the frequency of the motor rhythm in the reduced preparation ($r = +0.78$, $p \leq 0.01$). In the isolated CNS preparation, however, the correlation ($r = +0.35$) was not significantly different from zero ($p > 0.17$). The respective slopes were 126 and 90. The former (but not the latter) is significantly different from zero ($p \leq 0.01$), but the two slopes are not significantly different from zero ($p > 0.5$).

The phase position of SD activity—shown above to be a key criterion in distinguishing the different motor programs—was also examined in these experiments. In 23 episodes (14 preparations) of cyclic motor output caused by low voltage SGN stimulation in the isolated CNS, the SD discharged in phase with protractor activity in four trials, three of which are indicated by *solid symbols* in Figures 7 and 8 (the duty cycle could not be measured accurately in the fourth trial). The mean frequency of the motor rhythm in these four trials was 0.22 Hz, significantly different from the mean of the neutral rhythm(s) ($p \leq 0.01$) but not from that of the ingestion motor program in the isolated CNS ($p > 0.1$). Therefore, the motor program

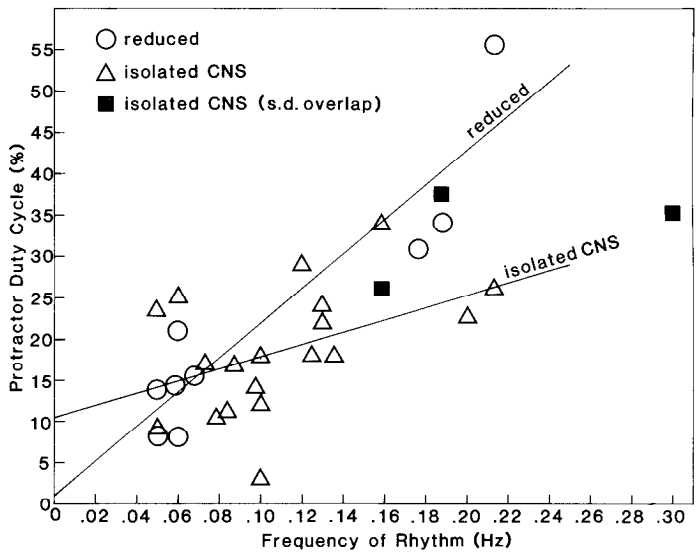

Figure 7. Mean protractor duty cycle plotted against the mean frequency of the motor rhythm for all episodes of the neutral rhythm(s). *Open circles* indicate the reduced preparation; *open triangles* indicate the isolated CNS; and *solid squares* indicate the isolated CNS during activity in which the SD discharged in phase with protractor activity (signifying the ingestion motor program). *Curves* were fitted by linear regression equations.

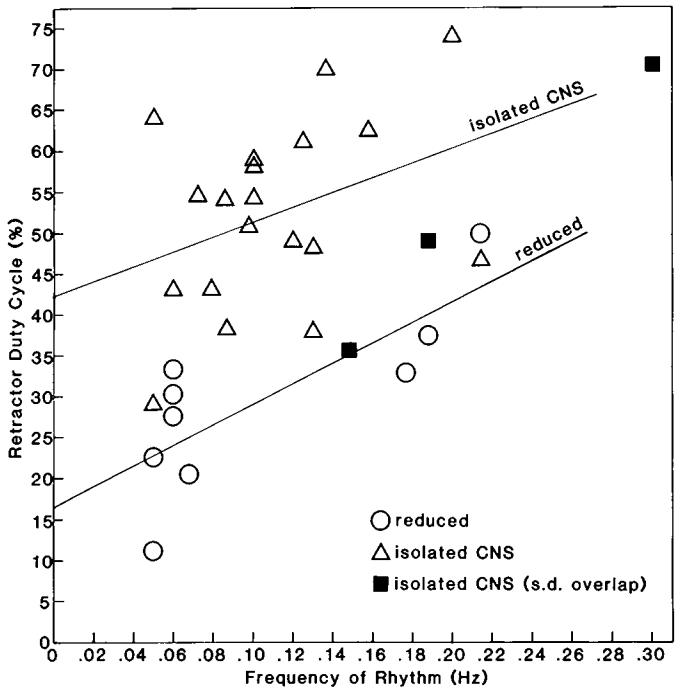

Figure 8. Mean retractor duty cycle plotted against the mean frequency of the motor rhythm for all episodes of the neutral rhythm(s). *Open circles* indicate the reduced preparation; *open triangles* indicate the isolated CNS; and *solid squares* indicate the isolated CNS during activity in which the SD discharged in phase with protractor activity (signifying the ingestion motor program). *Curves* were fitted by linear regression equations.

induced by low voltage SGN stimulation was indistinguishable from the ingestion motor program in 17% of the trials in the isolated CNS.

Discussion

We have now identified, characterized, and distinguished buccal motor programs in *Pleurobranchaea* using the intact, behaving organism (Croll and Davis, 1981), the reduced preparation (Croll and Davis, 1982), and the isolated CNS (this paper). These diverse approaches all yield the same conclusion, namely, that there are three such motor programs, corresponding to ingestion, egestion, and the "neutral" rhythm(s), and that all three motor programs are endogenous to the CNS.

Distinguishing features of buccal motor programs. The present study, in combination with previous work on the whole animal (Croll and Davis, 1981) and reduced preparations (Croll and Davis, 1982), furnishes qualitative and quantitative means to distinguish between the buccal motor programs. The ingestion and egestion motor programs are distinguishable in the reduced and/or isolated CNS preparation by six criteria: (*1*) the ingestion motor program is elicited by tonic CBC stimulation and sometimes by low voltage SGN stimulation, whereas the egestion motor program occurs spontaneously or in response to high voltage SGN stimulation; (*2*) the ingestion motor program is continuous whereas the egestion motor program occurs in stereotyped, triggered episodes of 5 to 15 cycles; (*3*) buccal retractor activity predominates during the ingestion motor program, whereas protractor activity predominates during the egestion motor program; (*4*) The SD (or SN) discharges during protractor activity during the ingestion motor program but is suppressed during the egestion motor program; (*5*) buccal constrictor m 5 discharges with retractor activity during the ingestion motor program but is suppressed during the egestion motor program; and (*6*) the protractor duty cycle is usually less than 50% during the ingestion motor program but greater than 50% during the egestion motor program. The latter criterion is, alone, a nearly 90% accurate indicator of the motor program.

The neutral rhythm(s) is qualitatively similar to the ingestion motor program, differing primarily in three regards: (*1*) the frequency of the rhythm is lower; (*2*) SD (or SN) activity is typically biphasic, occurring at the beginning and end of retractor discharge; and (*3*) the protractor duty cycle is less than 50%. The neutral rhythm(s) grades continuously into the ingestion motor program as the frequency of the rhythm increases, suggesting that it is a low intensity, behaviorally inefficacious version of the ingestion motor program. However, why the intact animal should routinely produce a behaviorally inefficacious motor program (Croll and Davis, 1981) is unclear.

Comparison with previous studies. Our investigations of buccal motor rhythms in *Pleurobranchaea* help clarify issues raised by McClellan's (1982a, b) studies on the same topic. In one respect, our conclusions agree; the motor pattern we term the "egestion motor program" appears to be identical to McClellan's "vomiting" motor pattern (Fig. 2*a* of McClellan, 1982a).

Our conclusions differ, however, in four other respects. First, McClellan (1982a, b) reports seven "buccal motor patterns," namely, biting, ingestion, vomiting, swallowing, writhing, rejection, and a primary rhythm. In contrast, we can rigorously distinguish only three buccal motor programs, corresponding to ingestion, egestion, and the neutral rhythm(s). This difference in conclusions appears to have resulted from the use of different methods of defining a motor program. McClellan (1982a, b) classified buccal motor programs according to accompanying behavior in the surgically reduced preparation, whereas we have defined a motor program according to spatiotemporal parameters of the motor output itself, accompanied by correlation with behavior in the intact animal. McClellan's approach is open to the ambiguity that a single motor program can accompany but not cause several unrelated behaviors. McClellan's "writhing in response to visceral distress," for example, is probably produced by body wall musculature, in which case it cannot be considered a buccal motor program.

Close examination of McClellan's published records of motor output shows that his biting and ingestion categories (McClellan, 1982a, Fig. 6*a1*) are indistinguishable from each other in terms of the motor output itself, and both appear to be similar to what we have termed the ingestion motor program. Similarly, McClellan's swallowing (McClellan, 1982a, Fig. 3), writhing (McClellan, 1982a, Fig. 3*b*), rejection (McClellan, 1982a, Fig. 6*b*), and primary rhythm (McClellan, 1982*b*, Fig. 1) all appear to be similar to each other in terms of motor output parameters and similar to the neutral rhythm(s) described here. Specific similarities include the following. (*1*) All entail cyclic discharge in the salivary duct, distinguishing them from the egestion motor program. (*2*) SD activity is in all cases monophasic and concurrent with retractor activity (McClellan's swallowing and primary rhythm) or biphasic (McClellan's rejection and writhing). Both patterns are characteristic of the neutral rhythm(s) (Croll and Davis, 1982, and this paper). (*3*) The mean protractor (m 2) duty cycle, calculated where possible from McClellan's published records, is 24% (swallowing) and 19% (writhing). Both values are diagnostic of the neutral rhythm (<33%) and dissimilar from the ingestion (33 to 50%) or egestion (>50%) motor program.

Therefore, when the parameters of the motor output itself are used as defining criteria, McClellan's (1982a, b) seven buccal motor patterns appear to be reducible to three categories, and these appear identical to the three motor programs we have been able to identify. We previously recognized that the neutral rhythm(s) may comprise more than one distinct motor program underlying more than one behavior (Croll and Davis, 1981). In addition, in the following paper (Croll et al., 1985a), we report

a "rebound" motor program that resembles an exaggerated form of the egestion motor program. Therefore, there may well exist more than three distinct buccal motor programs in *Pleurobranchaea,* but available data do not permit rigorous distinction of more than three.

A second difference between McClellan's and our conclusions deals with the ingestion motor program, which he reported could not be elicited from the isolated CNS (McClellan, 1982b, p. 206). Our studies show that the ingestion motor program can be elicited and rigorously distinguished from other motor programs, both in the reduced preparation (Croll and Davis, 1982) and in the isolated CNS (this paper).

Third, McClellan reported that vomiting motor activity (i.e., the egestion motor program) cannot be identified by buccal nerve root activity alone (McClellan, 1982b, p. 224). In the present work we have developed two criteria for identifying and distinguishing the egestion motor program based on extracellular recordings from a single buccal nerve, the protractor nerve (r 1). These criteria are the protractor duty cycle (>50% for the egestion motor program) and the episodic nature of the egestion motor program, which are, respectively, 88% and 100% reliable indicators of the egestion motor program. Re-examination of McClellan's six published records of r 1 activity during "vomiting" (McClellan, 1982b, Figs. 8, *b* and *c*, 9*b*, and 10, *a* to *c*) reveals that the protractor duty cycle exceeds 50% in 83% of his records, and the motor output is episodic in nature in all cases.

Fourth, in our original studies on the buccal motor system of *Pleurobranchaeae* (Davis et al., 1973), we described the cyclic motor output that results from low voltage SGN stimulation as a "feeding rhythm." McClellan (1982a, b), however, concluded that stimulation of this nerve elicits only a primary rhythm or vomiting and that the feeding rhythm we reported earlier was in fact vomiting (McClellan, 1982a, p. 207). As shown previously (Croll and Davis, 1982) and in the present paper, low voltage SGN stimulation causes either the neutral rhythm(s) (~80% of the cases) or the ingestion motor program (~20% of the cases), which is in most regards similar to the neutral rhythm(s). McClellan's published data are fully consistent with this interpretation (McClellan, 1982b, Fig. 8). Re-examination of our earlier published records shows that none of them exhibits the characteristic features of the egestion motor program. McClellan's (1982b) conclusion that SGN stimulation causes only a primary rhythm or vomiting may have resulted at least in part from the fact that he did not develop criteria for identifying the ingestion motor program in the isolated CNS preparation.

Central neural mechanisms of motor program switching. The present investigation, together with our previous studies of motor program switching in *Pleurobranchaea* (Croll and Davis, 1981, 1982), furnishes the necessary foundation for analyzing the neurophysiological mechanisms of motor program switching. Our demonstration that all three of *Pleurobranchaea*'s buccal motor programs can be reliably elicited and recognized in the isolated CNS preparation shows that multiple motor programs in this metastable motor system are all endogenous to the CNS. It follows that sensory feedback is not critical to motor program switching, although it has been shown that the different buccal motor programs can be triggered by different sensory inputs (Croll and Davis, 1982; McClellan, 1982a, b). This conclusion encourages a search for the neural mechanisms of motor program switching within the CNS. This search is undertaken in the second and third papers of this series (Croll et al., 1985a, b), which suggest that the ingestion and egestion motor programs are activated by different and nonoverlapping central "command" systems.

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