works containing more than one instance of hand preference, only one example was counted and scored. The case to be scored was selected by means of a random number table that was used to determine the quadrant (or subquadrant) within the picture to be searched and recorded.

By means of these selection procedures, 1180 scorable instances were found. Of these, 92.6 percent depicted the use of the right hand. There is no systematic trend toward increasing dextrality over the more than 50 centuries represented by this sample ($\chi^2 = 17.04$; d.f. = 15). To further demonstrate this point, our results were compared to a sample of contemporary laboratory and survey research on handedness. Hecaen and de Ajuriaguerra (*6*) have reviewed 48 such studies which yield a mean incidence of dextrality of 90.6 percent (median 93.4 percent) and a standard deviation of 7.5 percent. None of the historical periods shown in Table 1 deviate significantly from these values.

These data can also be evaluated for evidence of social pressures which might manifest themselves as cross-cultural rather than historical differences. Table 2 shows the division of the sample into geographical regions with the data collapsed across the temporal dimension. Once again, no clear differences emerge among the various cultural subgroupings ($\chi^2 = 8.14$, d.f. = 6).

If this apparent absence of any systematic changes in the distribution of hand preference over the past 50 centuries is considered in conjunction with the uniform distribution of dextrality regardless of geographical region, these results seem to support a physiological theory of handedness rather than one which proposed cultural and social determinants of handedness. Thus, as far as the historical record takes us, man appears to have always been right-handed.

Table 2. Geographical distribution of handedness as manifested by works of art.

Region	Sample size	Right-handed (%)
Central Europe	335	93
Mediterranean Europe	317	95
Middle East	89	96
Africa	117	90
Central Asia	101	92
Far East	139	91
Americas	82	88
Summary	1180	92.6

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Behavioral Choice: Neural Mechanisms in *Pleurobranchaea*

Abstract. *In the marine mollusk* Pleurobranchaea, *it is known that feeding occurs and withdrawal from tactile stimuli is suppressed when the sensory stimuli for feeding and withdrawal are presented simultaneously. This "dominance" of feeding behavior over withdrawal behavior occurs because the central nervous network controlling feeding inhibits the central nervous network controlling withdrawal. The inhibition is mediated by a bilaterally symmetrical pair of reidentifiable feeding neurons that are members of the "corollary discharge" population in the buccal ganglion. This study supports the hypothesis that inhibitory interactions between competing motor systems are responsible for the "singleness of action" that characterizes animal behavior.*

Sherrington observed that certain spinal reflexes are prepotent over others that employ the same motoneurons and concluded that the resultant "singleness of action" is the keystone to coordinated movement (*1*). Ethologists have since recognized that singleness of action applies also to the integrated behavior of the whole organism; indeed, a major issue in the study of behavior is the methods by which animals "decide" to perform a single behavioral act to the partial or complete exclusion of others (*2*). In the carnivorous marine gastropod *Pleurobranchaea*, such decisions are made in accord with a behavioral hierarchy (*3*), defined as the organization of unrelated acts of behavior into a priority sequence that governs behavioral choices. For example, when *Pleurobranchaea* is touched vigorously on the anterior oral veil, it withdraws from the tactile stimulus; when presented with squid extract, *Pleurobranchaea* exhibits a stereotyped, rhythmic feeding response (*3*, *4*). When touch and food are presented together, feeding is normally elicited and withdrawal is suppressed (*4*). Therefore, feeding is "dominant" over withdrawal in the behavioral hierarchy of *Pleurobranchaea*, an evolutionary adaptation that presumably prevents withdrawal from food.

Previous behavioral experiments (*4*) suggested that feeding dominates withdrawal because neurons that are part of the feeding system inhibit the withdrawal behavior. We have confirmed this hypothesis by identifying the inhibitory neurons that mediate the effect. Our study indicates that inhibitory interaction between different motor systems represents one neural mechanism underlying behavioral hierarchies.

Three types of preparations were employed in these experiments: the whole animal, the semi-intact animal, and the isolated central nervous system. Whole-animal preparations were made by exposing the cerebropleural ganglion (brain) by a 2-cm incision and suspending the animal in seawater by hooks attached to the margins of the opening (*5*). The brain was stabilized on a micromanipulated platform with small pins passed through the marginal connective tissue. Sensory and motor connections remained intact and operational for one to several hours in such preparations. Semi-intact preparations consisted of eviscerated animals whose nervous systems remained intact and connected as usual to feeding and withdrawal muscles (Fig. 1A). Such preparations were anchored to a base (Sylgard) by pins that passed through the foot. Isolated nervous systems (Fig. 1B) were prepared as detailed previously (*6*). All preparations were made from medium-sized specimens (volume, 100 ml) and submerged in filtered seawater at 13°C during experiments. Extracellular stimulation and recording from nerves mediating feeding and withdrawal was accomplished with glass capillary suction electrodes. Intracellular recording and stimulation of single neurons was accomplished with glass capillary microelectrodes filled

with 3*M* KCl (tip resistance, 1 to 20 megohms) and inserted into somata.

The central nervous component of feeding (rhythmic coordinated motor output in nerves that supply feeding muscles) can be elicited from an isolated nervous system preparation by extracellular stimulation of the stomatogastric nerve or nerves and monitored by extracellular recording from buccal nerve roots (*6*). In order to study the interaction of the feeding and local withdrawal systems, it was necessary to develop an analogous procedure for the local withdrawal system. The oral veil is innervated almost exclusively by two nerves, (i) the small oral veil nerve (SOVN) and (ii) the large oral veil nerve (LOVN) (*6*). Bilateral lesion of these two nerves eliminated approximately 90 percent of the central component of local withdrawal (*7*). Extracellular stimulation of the peripheral stump of a cut SOVN in a semi-intact preparation caused withdrawal of the oral veil, which shows that the SOVN contains at least some efferent neurons responsible for withdrawal. Extracellular recording from the peripheral stump of a cut LOVN revealed vigorous afferent discharge in response to tactile stimulation of the oral veil, which shows that the LOVN carries sensory information of the type that causes withdrawal, as previously reported (*8*).

These observations suggest that (i) centripetal stimulation of the LOVN might provide one reliable means of experimentally eliciting the withdrawal response and (ii) efferent discharge in the SOVN might provide a measure of local withdrawal behavior. We therefore performed experiments which showed (i) that electrical stimulation (a 1-second series of rectangular pulses, 1-msec duration, 10 to 15 volts, 10 hertz) of the cut central stump of the LOVN of an otherwise intact preparation invariably caused only a local withdrawal of the head and oral veil and (ii) that this response was qualitatively indistinguishable from that caused by tactile stimulation of the oral veil. The number of action potentials in the efferent response recorded extracellularly from the cut central stump of an SOVN in an otherwise intact preparation during the 5 seconds following natural tactile stimulation of the oral veil was highly correlated with the amplitude of local withdrawal as recorded under low-power magnification using an ocular micrometer ($r = .94$, $N = 120$, four preparations). These experiments show that there is a central nervous component of withdrawal behavior that can be elicited by LOVN stimulation and effectively monitored by recording from the SOVN.

To extend these observations to the isolated nervous system preparation, the LOVN was stimulated according to parameters identical to those that caused withdrawal in the whole animal preparation, while extracellular recordings were again made from the SOVN. These recordings revealed an efferent response to LOVN stimulation that was qualitatively indistinguishable from that shown to correlate highly with the withdrawal response of whole animal preparations. We conclude that at the very least, this SOVN response (which we term "withdrawal output") is an adequate measure of activity in central neurons controlling withdrawal behavior. It further seems likely that this SOVN activity represents a portion of the central component of withdrawal behavior, although this has not been proved.

Following the above experiments, the interaction between feeding and withdrawal was studied in 12 semi-intact preparations. In each, electrical stimulation of the LOVN according to the original stimulus parameters, caused the characteristic SOVN activity accompanied by a withdrawal response (Fig. 1A, trace i). When the feeding rhythm was then elicited by stomatogastric nerve stimulation, electrical stimulation of the same LOVN through the same electrode and with the same stimulus parameters caused little or no efferent withdrawal output in the SOVN, and the withdrawal response of the oral veil was correspondingly weak or absent (Fig. 1A, trace ii). Stomatogastric nerve stimulation was then terminated and the feeding rhythm allowed to subside (15 seconds to 3 minutes). Restimulation of the LOVN following cessation of feeding output invariably showed that both the withdraw-

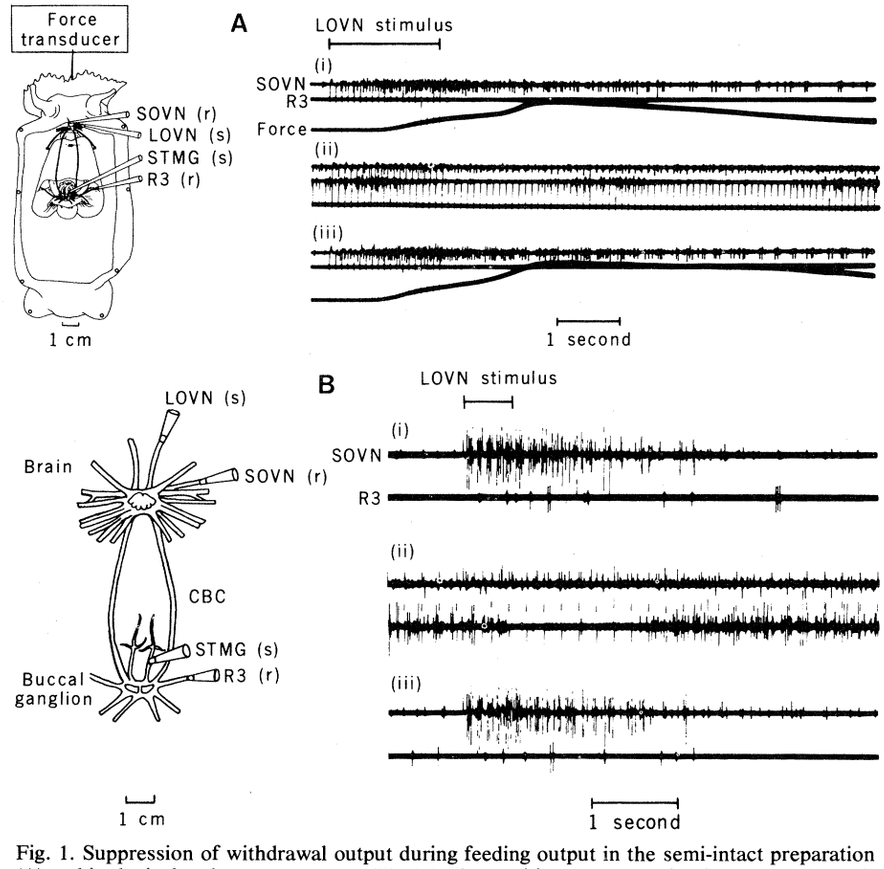

Fig. 1. Suppression of withdrawal output during feeding output in the semi-intact preparation (A) and in the isolated nervous system (B). (A) The semi-intact preparation is drawn schematically on the left, with extracellular suction electrodes in place on the small oral veil nerve (SOVN) and large oral veil nerve (LOVN) of the brain, and the stomatogastric nerve (STMG) and third root (*R3*) of the buccal ganglion. Nerves were stimulated (*s*) or recorded from (*r*). On the right are three traces showing withdrawal output induced by LOVN stimulus (bar above trace, in register with stimulus for all traces), before (*i*), during (*ii*) and immediately after (*iii*) feeding output was elicited by stimulating the STMG nerve. Withdrawal output was monitored by recording the efferent discharge from the cut central stump of one SOVN and by recording the force produced by the withdrawing oral veil (force; upward deflection = withdrawal). (B) The isolated nervous system preparation is drawn schematically on the left, with extracellular suction electrodes in place on the same nerves as in (A). Traces on the right show withdrawal output induced by LOVN stimulus (bar above traces) as in (A). Withdrawal output in isolated nervous systems was monitored by recording the characteristic efferent withdrawal burst from the SOVN. Abbreviation: CBC, cerebrobuccal connective.

al motor output recorded from the SOVN and the resulting behavioral response had fully recovered (Fig. 1A, trace iii). These results establish that the occurrence of feeding output is accompanied by suppression of withdrawal output, in accordance with earlier behavioral observations (*4*), and furnish a "bridge" from the behaving whole animal preparation to the isolated nervous system.

An analogous series of experiments was performed on the isolated nervous system. The characteristic burst of SOVN withdrawal activity (Fig. 1B, trace i) caused by stimulation of the LOVN (stimulus parameters identical to those described above for the whole animal preparation) was absent during feeding output (Fig. 1B, trace ii) but returned immediately on cessation of feeding output (Fig. 1B, trace iii). These results, obtained in all 12 isolated nervous systems examined, establish that the suppression of withdrawal output during feeding output does not depend upon proprioceptive return from the rhythmic feeding movements. They indicate instead that the dominance of feeding over withdrawal is mediated at least in part by purely central processes.

In order to determine the central nervous mechanisms underlying the dominance of feeding over withdrawal, the stimulus for the withdrawal output in the isolated nervous system (electrical stimulation of the cut LOVN using the same parameters as in the whole animal preparation) was delivered before, during, and after intracellular stimulation of single neurons in the central network that controls feeding. Using this procedure, we located a neuron in the buccal ganglion of ten isolated nervous system preparations that, when stimulated, suppressed LOVN-initiated withdrawal output. This cell was found on both sides of the buccal ganglion in the same relative position and is thus presumably a member of a bilaterally symmetrical pair of neurons. In addition to the apparently unique property of suppressing withdrawal, either of these paired cells was reliably identified by the following properties: (i) The neuron is a member of the previously identified corollary discharge (CD) population (*6*, *8*); as such, it sends an ascending axon to the brain through the cerebrobuccal connective as shown by orthodromic and antidromic stimulation. (ii) The soma of the neuron in question was 10 to 30 μm in diameter and located at the extreme anteriomedial margin of the CD population (Fig. 2). (iii) The neuron receives similar synaptic inputs in all preparations, including a large (1- to 5-mv) excitatory postsynaptic potential (EPSP) in response to stomatogastric nerve stimulation (rectangular pulse 7 volts in amplitude and 1.25 msec in duration), a burst of several small (0.1 mv) EPSP's during the late withdrawal phase of the feeding rhythm, and a small (0.1-mv) but long-lasting (1 second) hyperpolarization in response to activation of withdrawal by LOVN stimulation. This neuron is therefore reidentifiable on the basis of several anatomical and electrophysiological criteria.

Intracellular stimulation of one of these paired neurons at 10 to 20 impulses per second characteristically reduced the LOVN-initiated withdrawal response to about half the normal (control) level and sometimes abolished withdrawal output completely (Fig. 2B). These same neurons were active at comparable discharge frequencies during feeding output (Fig. 2C). Hyperpolarization of a single member of the pair of neurons during feeding output silenced the neuron and simultaneously restored the LOVN-driven withdrawal response to near control levels (Fig. 2D). Technical problems have so far prevented simultaneous penetration of both members of this pair of CD cells. Since intracellular stimulation of either cell alone causes substantial (at least 50 percent) suppression of the local withdrawal response, we assume that the effects of both of these cells, acting in concert, would sum to cause a greater suppression of withdrawal than does either cell alone. Even if the inhibitory effects of the two cells are only partially additive, however, the evidence indicates that this pair of cells is both necessary and sufficient to account for the suppression of withdrawal output during feeding output.

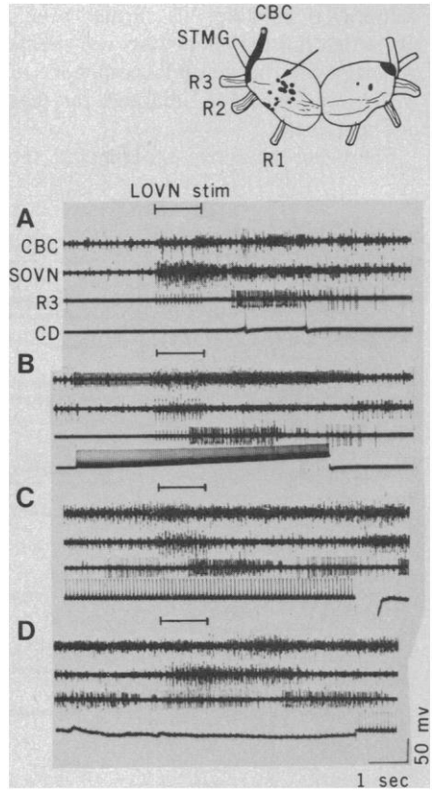

Fig. 2. Demonstration that the identified corollary discharge (CD) cell is necessary and sufficient to suppress local withdrawal output induced by LOVN stimulation (bars above records) in an isolated nervous system preparation. At the top is a tracing of a buccal ganglion as seen in ventral aspect following cobaltous chloride "back-injection" of the CBC, and showing the somata of the corollary discharge neurons (*6*, *9*) that send axons to the brain. Arrow indicates the usual position of the neuron whose effects are illustrated below the tracing. Traces A and B, which are continuous records, show the efferent withdrawal output in the SOVN in the absence (A) and presence (B) of CD neuron activity caused by intracellular current injection. Traces C and D, also continuous records, show withdrawal output during feeding output when the CD neuron is allowed to fire spontaneously at "physiological" frequencies (C) or is suppressed by injection of hyperpolarizing current (D). Stimulation of a single corollary discharge neuron typically reduced the amplitude of the withdrawal burst by at least 50 percent.

The findings provide a probable neurophysiological explanation for a simple form of behavioral choice by demonstrating suppression of a subordinate motor system (withdrawal) by neurons in a dominant motor system (feeding). Similar inhibitory interactions between central networks of neurons controlling different behaviors may underlie not only behavioral heirarchies, as suggested here, but also other related ethological and psychological phenomena, such as choice, behavioral switching and gating, and selective perception and attention.

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