

ABSTRACT. Computational neuroethology is the computer simulation of the neural control of behavior of simpler whole animals. An object-oriented model of the nutritional physiology of the blowfly *Phormia regina* illustrates the biological basis of the regulation of feeding behavior in such models, using the message-passing features of object-oriented programming as an analogy of biological message-passing. The model predicts the pattern of stimulation of the foregut and abdominal stretch receptors that regulate the insect's level of activity and responsiveness to stimuli.

Message-passing features of object-oriented programming were used to simulate three major physiological message-passing methods: electro-chemical (nerve impulses), chemical (hormones, synaptic neurotransmitters, and biochemical by-products), and physical (stretch response and hydrostatic pressure effects). Object-oriented programming facilitates depiction of the anatomical locations of physiological and biochemical processes.

The Object-Oriented Blowfly: A Study in Computational Neuroethology

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The field of robotics abounds with biological analogies. Insect-like autonomous robots capable of simple autonomous behaviors have been constructed (Brooks 1989, Connell 1987), and robotic applications currently being developed in the agriculture and food industries (Gandolfo and Sandini 1991) have parts that mimic biological functions (Vassura 1991). The behavior of autonomous robots must be goal-oriented, adaptive, opportunistic, plastic, and robust: issues for which nervous systems have evolved (Beer 1990).

Beer (1990) proposed construction of autonomous robots, which are controlled by artificial nervous systems whose design has been abstracted from biological nervous systems, and developed a computer simulation of insect locomotion and feeding behaviors and their control by an artificial nervous system. In that study, *computational neuroethology* was defined as the computer simulation of the neural control of behavior in simpler whole animals (Beer 1990). A key feature of his system was the feedback from digestion regulating the feeding behavior.

In his discussion, Beer (1990) regretted that his artificial insect's nervous system was *ad hoc*, with parts developed in

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a "neurobiologically plausible" fashion, and suggested that "Only further study of natural nervous systems and considerably more design experience with artificial ones will increase the sophistication of these designs, and deepen the principles on which they are based."

Webster's Third New International Dictionary (1971) defines "message" as "a unit of information that is received by a sensory organ, is transmitted centrally in the nervous system, and functions as a stimulus," or as "transmitted information sent by messenger or by some other means (as by signals)" with "signal" having the meaning "something that incites to action" or "a detectable physical quantity or impulse ... by which messages or information can be transmitted." In the field of computing, message passing is a fundamental concept of the object-oriented paradigm, with an object-oriented system being described as "a set of objects communicating with each other to achieve some result" (LaLonde and Pugh 1990).

In this regard, the different parts of the digestive system, the nervous system and the endocrine system, organs such as the fat body, as well as muscles and blood can all be considered objects. Material processed by one of these objects may be passed to another object, acting as a signal or message and triggering a set of activities by the receiving object. The nature and magnitude of these activities depends on the information contained in the message.

The present study reviews the neural control of insect behavior, with a view to providing a firmer biological basis for future studies in computational neuroethology. The study focuses on the blowfly *Phormia regina* Meigen (Diptera: Calliphoridae), which has one of the best-studied insect nervous systems (Dethier 1968, 1969, 1971; Fredman 1975; Gelperin 1971, 1972; Getting 1971; Green 1964a, b; Thomson 1977a, b). To provide a focus for the review, an object-oriented model of blowfly nutritional physiolo-

gy was developed, using the message-passing features of object-oriented programming as an analogy of biological message passing.

Blowfly Feeding Behavior

The feeding process is initiated by stimulation of sensory hairs on the tarsi. Each hair contains five receptors, responding to sugar, salt, water, mechanical stimulation, and anions, respectively (Dethier 1969). Appropriate stimulation of even a single hair induces the fly to extend its proboscis, bringing sensory hairs on the labellar lobes in contact with the food. Stimulation of even a single labellar hair then induces opening of the labellar lobes, bringing labellar papillae into contact with the food. Stimulation of these papillae leads to activation of the cibarial pump, leading to ingestion.

The nature of the food is thus monitored at three levels, with stimulation in excess of the current feeding threshold being required at each level (Dethier 1969). Neural feedback from stretch receptors in the foregut and abdomen regulates the feeding threshold by monitoring the volume of the crop contents and the rate of crop emptying, which, in turn, is regulated by a nutritional feedback mechanism related to the properties of the food. The mechanism of the ingestion and crop-emptying processes has been investigated and quantified (Thomson 1975a, b, 1977a, b; Thomson and Holling 1974, 1975a, b, 1976a, b, 1977), permitting prediction of foregut activity patterns given a wide range of diets.

Neural feedback from the foregut stretch receptors also determines the rate of release of a hormone that regulates overall activity patterns (Green 1964a, b). Blowfly activity patterns and flight dynamics were studied by Thomson and Holling (1976c) and Thomson and Thompson (1977).

The Blowfly Digestive System

The muscles of the blowfly digestive system are stretch-sensitive, due to the properties of the muscle membrane, responding to stretching by

contracting, and are organized to function as five valves and five pumps (Fig. 1) (Thomson 1975b). Synchronous function of the system is initiated by crop (P5) contraction. The crop, pump P4, and peristaltic waves in the crop duct (P3) act together with valves V3 and V4 to maintain waves of pressure against valve V2. Note the analogy between the peristalsis in the crop duct and the mechanism described for a fruit-swallowing oesophagus for a peach-picker robot arm (Vassura 1991).

Slugs of fluid passing through V2 stimulate contraction of the muscles of pump P2 (the post-ganglionic region of the oesophagus), which then empties through valve V5 into the midgut. Stretch receptors in the walls of P2 monitor the frequency of filling of this pump. Other stretch receptors lying below the crop and in the walls of the abdomen monitor crop volume and contraction (Dethier 1969).

Neural Parameters

Beer (1990) developed model neural circuits constructed of sensory and motor neurons with at least five electrically-based parameters: membrane conductance, membrane capacitance, minimum firing frequency (usually zero), threshold voltage, and gain. Sensory neurons were

modeled using an intrinsic current whose magnitude is a function of the intensity of a stimulus, while motor neurons had effector functions that related firing frequency to some physical quantity. Connections between neurons had different weightings for triggering activity across the simulated synapse. Cells defined as pacemakers and random burst generators have high and low intrinsic currents, and trigger neurons have a single intrinsic current whose magnitude and duration are given.

Using the above approach, Beer was able to simulate an insect with a number of behaviors such as locomotion, edge-following, food-seeking, and feeding. The physiological state of satiation was also simulated. However, Beer's (1990) model does not readily capture the types of measurements made by physiologists. Perkel et al. (1968) list a wide range of potential neural codes for representing information in nervous systems (Table 1), and many of these have been investigated in the blowfly. For example, Gelperin (1972) measured the output of the foregut stretch receptor in terms of frequency of bursts of impulses as slugs of fluid passed through P2, and Getting (1971) studied the sensory control of motor output in fly proboscis extension through the temporal summation of sensory activity during a 20-millisecond period after stimulation of a single sensillum. There are

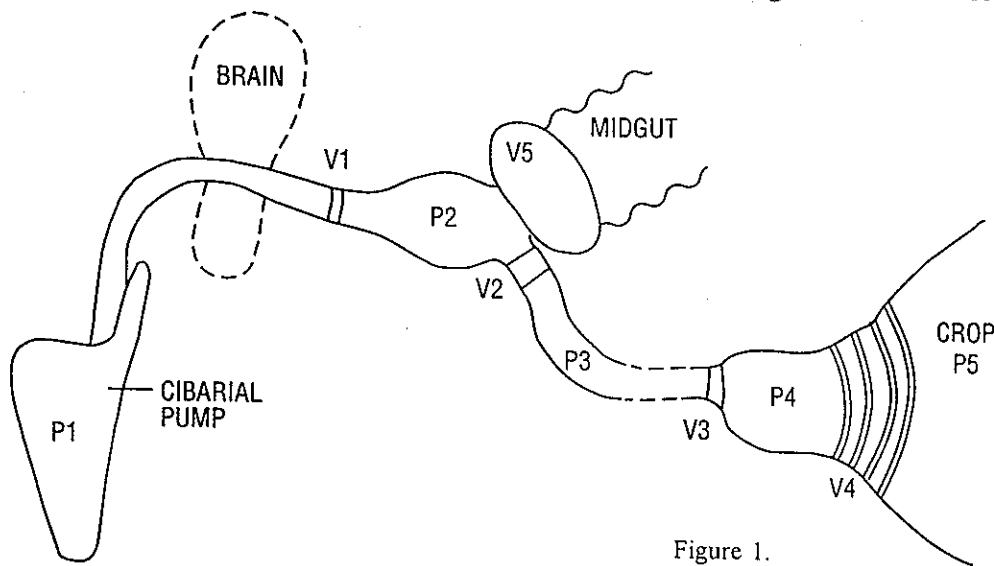


Figure 1.
Diagram of the valves (V1-V5) and pumps (P1-P5) in the foregut of *P. regina* (from Thomson 1975b).

Table 1. *Possible neural codes for representation of information in the nervous system (from Perkel et al. 1968).*

I. NEURONAL EVENTS OTHER THAN IMPULSES

A. Intracellular Events

1. Receptor potential: amplitude
2. Synaptic potential: amplitude
3. Synaptic conductance change: amplitude
4. Synaptic conductance change: spatial distribution
5. Membrane potential: spatial and temporal distribution
6. Graded potential in axonal terminals

B. Intercellular Events

1. Transmitter released
2. Potassium ion released
3. Neurosecretion released
4. Electrotonic coupling between specific cells
5. Electrotonic interaction via extracellular space

II. IMPULSES IN UNIT NEURONS

A. Representation by identity of active fiber

1. Labeled lines

B. Codes based on temporal properties of impulses

1. Time of occurrence
 - a. Instant of firing
 - b. Phase locking to stimulus
2. Interval statistics codes
 - a. Frequency: weighted average
 - b. Frequency: instantaneous
 - c. Frequency: increment above background
 - d. Frequency: rate of change
 - e. Frequency of firing/missing at fixed intervals
 - f. Coefficient of variation
 - g. Higher moments; interval histogram shape
3. Temporal pattern of impulses
4. Number of impulses or duration of burst
5. Velocity change in axon

C. Codes based on other properties

1. Amplitude change in axon
2. Spatial sequencing

III. ENSEMBLE ACTIVITY

A. Representation by spatial array

1. Topographic distribution of active fibers

B. Codes based on temporal relations among active channels

1. Latency distribution
2. Phase distribution
3. Probability of firing after stimulus: PST histogram shape

C. Representation by form of composite multiunit activity

1. Evoked potential shape
 2. Slow waves in ongoing EEG
-

therefore many different message formats that could be used to pass information from the sense cell to the brain. The message passed to the sense cell by the physiological systems of the insect determines the output message passed from the cell to the central nervous system.

Organisms face the task of extracting information about an unknown time-dependent stimulus from short segments of a spike train. The effect of noise level and fault tolerance of this process in blowfly neural code interpretation is discussed by Bialek et al. (1991). The manner in which a few sensory cells can discriminate among a wide range of stimuli is discussed by Dethier (1971), Ichikawa (1990, 1991) and O'Carroll (1993).

Options for simulating such processes include development of sensory cell objects, interneuron objects, central nervous system objects, and motor objects. Message-passing features could represent the spike trains passed between these objects, with methods attached to the objects to integrate and interpret the spike trains. Anatomical distributions of sense cells in relation to spatial interpretations could be handled by allocating sense cell objects to anatomical objects such as tarsi or labellae.

Object Representation of the Blowfly Nutritional System

The following model of blowfly nutritional physiology was developed. Following Thomson and Holling (1977), nutritional system dynamics depend primarily on P2, P5, and V2, with the functioning of V2 depending on the biochemistry of the blood and fatbody, and on the overall metabolic rate (primarily related to locomotion, especially flight). Passage of food through V5 to the midgut is automatic once P2 exerts its effect.

The code, written using the object-oriented extensions of THINK C™ (Symantec Corporation, Cupertino, California), of the main routine of a program for simulating blowfly carbohydrate nutrition (Fig. 2) indicates the major objects, and the message passing that synchronizes their operation. The main routine of the program is relatively simple, the complexity of the pro-

cesses being handled by the methods that are attached to the objects, as described below.

Ingestion of a meal effectively "primes" the pump representing the crop with a volume equal to the meal size, and the blood osmotic pressure and trehalose (blood sugar) synthesis rate are established. The code (Fig. 2) illustrates different approaches to the programming of the object attributes. Data in a class can have public access such as `crop->volume` or private access, controlled by public functions such as `blood->GetOP()` for access to the blood osmotic pressure. Message passing is abstracted to the level at which data or estimates are available. Thus, crop volume is passed as a message in place of the actual message which comprises crop pressure, volume change in the crop duct, and pressure changes and physical distortion resulting from peristalsis in the crop duct. Note that, in larger insects, pressure changes in the gut can be measured (Davey and Treherne 1964).

The digestive cycle starts with passage of a slug of fluid through V2, with the slug volume ($V(V2)$) being determined by the pressure exerted by the crop, which in turn is a function of crop volume (CVOL) (Thomson and Holling 1977):

$$V(V2)_{\max} = 0.012 \mu\text{l} \quad [1a]$$

$$V(V2) = 0.002 \mu\text{l}, \quad \text{CVOL} \leq 1 \mu\text{l} \quad [1b]$$

$$V(V2) = V(V2)_{\max}(1 - e^{-0.18\text{CVOL}}), \quad \text{CVOL} > 1 \mu\text{l} \quad [1c]$$

Several physically-based message-passing methods are abstracted in these equations which are included in the method `GetV2SlugVolume(crop->volume)` of the `valve2` object (Fig. 2): hydrostatic pressure changes due to crop contraction can transmit information; volumes of material can move from one object to another, physically distorting them; and contraction of a muscle fiber sends messages to adjacent muscle fibers by virtue of their physical attachment distorting the muscle membrane, as in the propagation of a peristaltic wave in the crop duct (P3). The sugar content of the slug acts as a chemical message that is passed to the blood, based on the slug volume, the molarity of the solution, and the molecular weight of the sugar.

Two chemical messages, the slug sugar content and blood osmotic pressure, and a physical

message based on the crop volume, combine to determine the time until passage of the next slug of fluid in the method `GetValveTime` of the `valve2` object. The time between slugs (t') was defined by Thomson and Holling (1977) as

$$t' = \frac{1 + 1.79Q}{(y_{\max} - 13.5OP) \cdot \beta(\text{CVOL})^{1/2}} - \frac{1}{(y_{\max} - 13.5OP)} \quad [2a]$$

where Q is the μg of sugar in the slug, OP is the blood osmotic pressure, and $CVOL$ is the crop volume. β and y_{\max} are empirical parameters. Each slug of fluid passing through pump P2 into the midgut reduces the crop volume.

Three physiological processes, the basal metabolism of the muscles, trehalose synthesis, and glycogen synthesis, compete for the sugar in the slug which passes from P2 through V5

```

// Initialization
p2->PrimePump(0.0);
crop->PrimePump(CVOL0);
blood->OPUpdate();
blood->SetRTr();

/** Main loop. */
while (crop->volume > 0.1)
{
    // get slug volume
    slug = valve2->GetV2SlugVolume(crop->volume);

    // set sugar content of slug
    valve2->SlugSugar(slug, molarity, mwt);

    // get time to next slug
    deltatime = valve2->GetValveTime(valve2->GetSlugSugar(),
                                     blood->GetOP(), crop->volume);

    // update crop volume
    crop->RemoveSlug(slug);

    // set trehalose conversion rate
    blood->SetRTr();

    // update trehalose concentration
    blood->TrUpdate(muscle->GetBmr(),
                   valve2->GetSlugSugar(), deltatime);

    // update blood osmotic pressure
    blood->OPUpdate();

    // update glycogen
    fatbody->GlycUpdate(muscle->GetBmr(),
                       valve2->GetSlugSugar(),
                       deltatime, blood->GetRTr());

    // update time
    clock1->ClockAdvance(deltatime);
}

```

Figure 2.

Code for the main program for simulation of blowfly carbohydrate nutrition, using the object oriented extensions of THINK C™.

into the midgut then diffuses from the midgut into the blood. The basal metabolism, especially of the flight muscles during flight, has first call on the available sugar, to the extent that equation [2] was modified by Thomson and Holling (1977) to reduce the influence of Q by the metabolic rate (MR) between slugs:

$$t_h = \frac{1 + 1.79(Q - MR \cdot t_{h-1})}{(y_{\max} - 13.5OP) \cdot \beta(CVOL)^{1/2}} - \frac{1}{(y_{\max} - 13.5OP)} \quad [2b]$$

The proportion of the remaining sugar converted to trehalose is defined by the method `SetRtr()` of the blood object. Note that, for simplicity, the trehalose synthesis is carried out in the blood object rather than defining separate tissue objects to do the synthesis and pass the new trehalose to the blood. The proportion of sugar converted to trehalose ($R(TR)$) was defined by Thomson and Holling (1977) as

$$R(TR) = R(TR)_{\max} e^{-0.15TR} \quad [3]$$

where TR is the current trehalose concentration. Any remaining sugar is converted to glycogen in the fat body, while if the sugar in the slug is insufficient to meet the insect's basal metabolic requirements, the difference is made up mainly by metabolism of glycogen, and to a small extent by the metabolism of trehalose. Changes in osmotic pressure of the blood are essentially determined by the trehalose concentration.

The mechanism, hypothesized by Thomson and Holling (1977), by which the basal metabolic rate pre-empts the sugar from the slug passing to the midgut, is not made explicit in equation [2b]. The midgut of the blowfly consists of three distinct anatomical regions: the thoracic ventriculus, the abdominal ventriculus, and the helicoid region which also lies in the abdomen. Fluid takes some time to pass from the thoracic ventriculus to the abdominal ventriculus, resulting in most sugar from the slug diffusing into the hemolymph in the thorax, where the flight muscles are located, while the sites of trehalose and glycogen synthesis are in the abdominal fat body.

There is only a narrow opening between the thorax and abdomen through which hemolymph mixing can occur between the thorax and abdomen, resulting in a physical constraint on the access of the trehalose and glycogen synthesis systems to the dietary sugar. Friedman (1967) concluded that the rate of trehalose synthesis by the fat body was determined by the local concentration of trehalose surrounding the organ. Object-oriented modeling of the system would facilitate explicit representation of this situation. For example, separate blood objects "thoracic_hemolymph" and "abdominal_hem-olymph" could be defined, with an appropriate method to define the mixing rate between them, and specific anatomical locations defined for the different midgut regions and the fat body. However, such changes would require data not currently available. Using the system as described above, the frequency with which slugs of fluid pass through pump P2 into the midgut can be predicted for different diets (Fig. 3).

Relating Nutrition to Feeding Threshold

Consideration of the neural mechanisms and the nutritional physiological processes in terms of message passing permits new evaluation of hypotheses discussed in the literature. The role of feedback from the abdominal and foregut stretch receptors has been determined from experiments in which hyperphagia followed cutting of the recurrent or abdominal nerves. Getting (1971) proposed a neuronal model for regulation of blowfly feeding behavior in which sensory input from sugar receptors was summed by an interneuron on which input from the foregut stretch receptors exerted a direct inhibitory effect, implying that the greater the neural feedback, the greater the inhibition and the higher the feeding threshold.

However, the crop empties faster with dilute solutions than with concentrated solutions, and would therefore appear to be providing a large amount of inhibitory feedback at a time when the feeding threshold is low (Fig. 3). The converse is true for the concentrated solution. The

underlying message-passing parameters of this paradox could not be identified in the present study.

An alternative model of sensory feedback was suggested by Gelperin (1972), based on slugs of concentrated sugar solution being rapidly shuttled back and forward between the foregut (P2) and crop duct (P3) through valve V2, with only occasional slugs being passed through V5 from P2 to the midgut. This pattern of gut activity would provide a high level of sensory feedback with concentrated solutions. Neither Dethier (1969) nor Thomson (1975b) reported this type of gut activity; however, Thomson (1975a) demonstrated that changes in the physiological solution used to moisten the tissues of the gut can change the pattern of foregut muscle activity, and this may explain the differences among studies.

Based on existing experimental evidence, it has not been possible to specify the manner in which messages from the foregut and abdominal receptors actually set the feeding threshold. However, the above discussion illustrates how the object-oriented approach to system development, with its focus on message passing, fa-

cilitated the consideration and integration of existing knowledge.

Although we do not fully understand the regulatory mechanism, some of the following observations may play a part in that process. Gelperin (1972) suggests that the foregut receptors are most important at low crop volumes when the crop was insufficiently swollen to stimulate the abdominal stretch receptors. If this is the case, slug shuttling back and forth might not be relevant to threshold setting. The idea of different sensory systems being important at different parts of a stimulus range is an appealing one for use in robotics.

Fredman (1975) indicates that the same nerve may serve either an excitatory or inhibitory function, depending on circumstances. Figure 3 might suggest such an excitatory function of the foregut receptor if it were not for the evidence that lesions of the recurrent nerve results in hyperphagia. Finally, changes in the crop contraction rate due to changes in the hemolymph sugars (Thomson 1975a) may cause bursts of activity in the abdominal stretch receptors to be superimposed on the background activity due to the crop volume, and threshold may be deter-

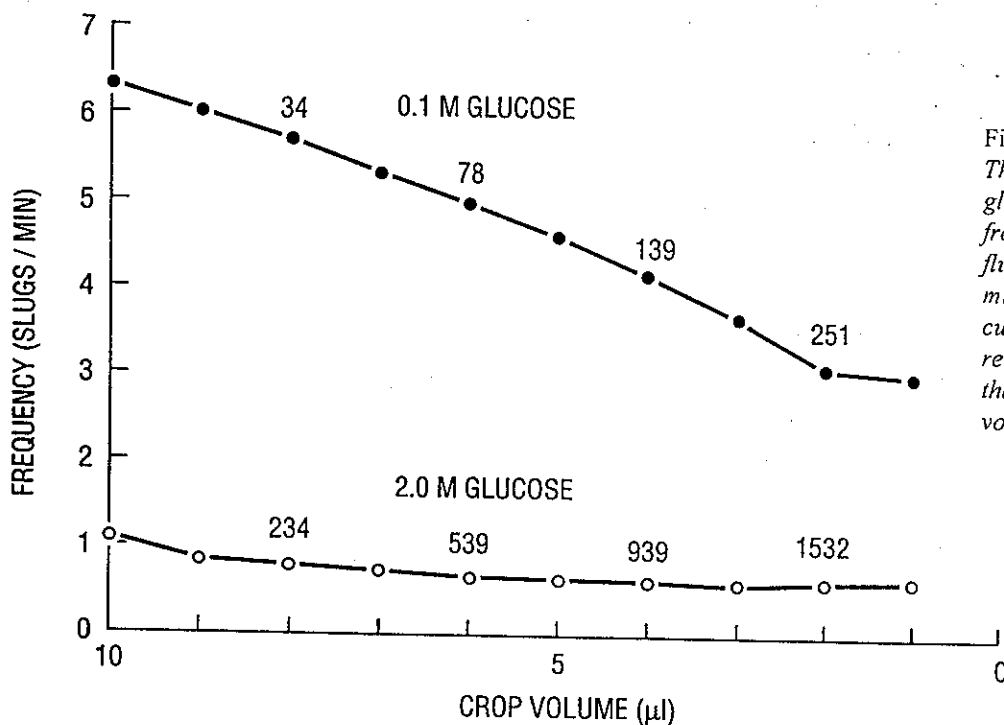


Figure 3. The effect of molarity of the glucose meal on the predicted frequency with which slugs of fluid pass from pump P2 to the midgut. The numbers on the curves indicate the minutes required for the crop to empty to that point from the initial meal volume of 10 μ l.

mined by the pattern of these bursts. All of these messages are possible under the scheme suggested by Perkel et al. (1968) (Table 1).

Hormones and Chemical Messages

A hormone can be defined as "An organic substance produced in minute quantity in one part of an organism and transported to other parts where it exerts a profound effect" (Abercrombie et al. 1951). The relative magnitude of the message and its effect distinguishes hormones from other chemical messages, such as the feedback from blood trehalose to rate of valve function in the blowfly gut, where a large amount of substance is required to cause the effect. The distinction between hormones and other chemical messages is not absolute; for example, only a small amount of acetylcholine is required to transmit a nerve message. The basic approach to simulation of hormonal and chemical message passing is similar to cases already described, differences lying mainly in the methods attached to objects for interpreting the messages.

Chemical messages can be categorized into those which result in a varying response over a continuum, dependent on the concentration of the chemical, and those for which the response is all-or-nothing. Synaptic transmitters would fall in this last category, where insufficient chemical messages fail to induce spike propagation across the synapse. Note that a single chemical can have multiple messages, as where blood trehalose can have a direct effect on chemical processes by virtue of its concentration, but it can also have an effect by virtue of its role in setting the effective osmotic pressure of the blood. The object-oriented approach, with its emphasis on message passing, assists in clarifying and handling such issues.

Autonomous Agents and Population Dynamics

The nervous systems of simple organisms have been used as models of robot control systems. To shed new light on such control sys-

tems, Beer (1990), who defined the term "computational neuroethology" in relation to a simulated insect displaying simple behaviors, advocates exploration of the neural implementation of more sophisticated behaviors, to the extent that different species of artificial organisms would interact and evolve within a simulated environment. At the simplest level in a single species, such studies could deal with relationships of activity patterns to crowding (Thomson and Holling 1976c), then move to more complex examples. One of the best-known examples of signal-passing in insects is the dance of the bees, which communicates food quality, distance, and direction. This behavior is rooted in the same physiological processes exhibited in flies responding to sugar solutions (Dethier 1957).

A multiple-species scenario might be to simulate on the computer an experiment such as that described by Pimentel and Soans (1971). They described a unique experiment on plant population adaptation in relation to feeding pressure, using flies feeding on tubes of sugar solution in which the salt content varied according to a simple genetic model. Computer simulation of patterns of insect locomotion have been carried out by Murdie and Hassell (1973), working with flies, but without explicit consideration of the underlying neural mechanisms. As indicated in the current study, we are now able to simulate much of the underlying insect physiology. AI studies dealing with autonomous agents (Caloud and Choi 1990, Steeb et al. 1986) would be relevant here.

Discussion

If we had perfect knowledge of the sensory control of insect feeding behavior, we would be able to specify the impulse patterns being passed from the sense organs through interneurons to the brain. We could then specify a method by which the information in the neural code is extracted and modified in relation to neural feedback, and use that information to generate the nerve message passed to the effector organ. In practice, however, our knowledge is limited and we know only that the impulse pattern is an un-

known function of some property such as crop volume. In empirical simulations, properties such as crop volume act as a surrogate message passed to other objects in place of the impulse pattern from the abdominal stretch receptors or the pressure waves resulting from crop contraction. Object-oriented programming facilitates use of actual nerve impulse patterns, as well as such surrogate messages, while making anatomical effects explicit.

The three main properties that characterize object-oriented programming language are encapsulation, inheritance, and polymorphism. Encapsulation combines a data structure with the functions (methods) dedicated to manipulating the data. Encapsulation was used throughout the present example, with illustrations of varying modes of data access through public and private methods.

One can build new, derived classes from original base classes, creating a hierarchy of classes with inheritance of data and functions from these base classes. Polymorphism is where a method's name is shared up and down a class hierarchy, with each class in the hierarchy implementing the method in a way appropriate to itself. Neither inheritance nor polymorphism played a significant role in the present study.

The temporal sequence of events in the digestive process led to the construction of a main program that was procedural in appearance (Fig. 2) to address the synchronization of events, rather than construction of a clock object, which can be a complex process in its own right, as illustrated by LaLonde and Pugh (1990). Other procedural-like structures include methods such as `GetV2SlugVolume(cropvolume)` which in effect is like passing parameters to a function. The use of C++ to develop systems permits this mixing of object-oriented and procedural approaches.

Focusing on message passing, in the present study observations of crop-emptying rates in normal insects could not be reconciled with lesion studies such as those of Gelperin (1971, 1972), who made lesions of the nerves from the foregut and abdominal stretch receptors to demonstrate the role of these systems in regulating feeding threshold. Beer (1990) could evaluate

the effects of sensory lesions on the behavior of his simulated insect. One may speculate on the possibility that diagnostic systems analogous to those described by Self (1992) could be developed to define neural pathways based on their response to lesions.

"We need to find ways of formalizing our understanding the dynamics of interactions with the world so that we can build theoretical tools that will let us make predictions about the performance of our new robots" (Brooks 1991). Brooks (1986), with his "subsumption architecture," Beer (1990), and Connell (1990) all advocate an approach to robotics based on simple autonomous units passing messages among themselves. Connell (1990) specifically deals with *inhibitory* outputs, as well as outputs from modules that *suppress* the output of other modules. Information is passed as a stream of packets, which Connell graphically represents as a series of spikes similar to the spike pattern recorded in neurophysiological studies.

The literature on insect neurophysiology (Dethier 1969, Fredman 1975) deals extensively with neural message-passing phenomena such as sensory adaptation and habituation, and the formation of Central Excitatory States (CES). The CES may have an equivalent in the robotic short-term memory, but as yet there appear to be no robotic analogies to sensory adaptation and habituation, the equivalents to these functions being handled by central processors.

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