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[ESSAY]

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ABSTRACT—Arthropods have small but sophisticated brains which have enabled them to adapt their behavior to a diverse range of environments. The enormous evolutionary success of arthropods in terms of species richness and diversity depends on the sophistication of their brains. Advances in neurobiology have clarified some of the sensory and motor mechanisms of the arthropod brain, but the basic rules of computation underlying the central functions of the arthropod brain remain unknown. Consequently, it is not known how the basic design of the arthropod brain differs from, or is analogous to, that of other animals, especially mammals. In this report, we argue that characteristic features of the arthropod "microbrain" can be ascribed not only to the limited number of its constituting neurons but also to the optimization to life with a small body.

INTRODUCTION

Arthropods are the most diverse and abundant animal group representing about 80% of all known animal species (Wilson, 1988; Brusca and Brusca, 1990), and they play a vital role in the Earth's ecosystem. These animals have successfully adapted themselves to virtually every habitat and have developed amazingly diverse forms of behavior.

The diverse behavior of arthropods is all generated and controlled by their very small brains. The number of neurons contained in the arthropod brain is only 10^5–10^6 (Strausfeld, 1976), that is several orders of magnitude smaller than those of the mammalian brain (10^{10} in humans, Kandel *et al.*, 1991). Therefore, the information-processing capacity of the arthropod brain is much more limited than that of the mammalian brain and, consequently, arthropod behavior is more stereotyped and less flexible than that of mammals (Hoyle, 1976). Nevertheless, the arthropod brain is, no doubt, one of the most successful information-processing devices to have evolved on Earth. This is analogous to the fact that, while microcomputers have only a limited information processing capacity, compared with that of supercomputers, they can be adapted more easily to meet personal and business needs and, con-

sequently, play a vital role in the present human society. The arthropod brain, hereafter referred to as "microbrain," is a low-cost, light-weight, and compact information processing device, a masterpiece which has evolved by natural selection over a period of 500 million years. We argue here that the microbrain is optimized to fulfil functional requirements that are in part different from those for the mammalian brain, hereafter referred to as "megalobrain".

THE BRAIN AND EVOLUTIONARY SUCCESS OF ARTHROPODS

To attain insight into the design principles of arthropod "microbrain", we first discuss features which have made arthropods so successful. A hard exoskeleton protects them from predators and from physiological stress, movable jointed appendages with powerful striated muscles allow for fast movement; all features with selective advantages over other animals (Willmer, 1990; Brusca and Brusca, 1990). The small size of most arthropods, due probably to limitations imposed by mechanical properties of the exoskeleton (Currey 1967; Schmidt-Nielsen 1986), is also an important determinant of species richness, because there are many more niches in any given environment for small animals to survive and develop (Pianka, 1970; May, 1978; Gullan and Cranston, 1994). In general, rapid motion requires good coordination of the appendages, and utilization of microhabitats requires the ability

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to recognize and respond to different environmental factors. Thus, the success of arthropods depends on sophistication of the nervous system.

The argument that the evolutionary success of arthropods has crucially depended upon the sophistication of the nervous system is supported by consideration of the reasons for the success of insects, the most prosperous group of arthropods that represent 90% of their total species (Wilson, 1988). The high species diversity of insects has been attributed, at least in part, to the following factors (Wessells and Hopson, 1988; Peters, 1988; Gullan and Cranston, 1994). First, the acquisition of wings in the adult stage enables insects to disperse more easily. The development of flight requires the development of a nervous system that can rapidly perceive visual and mechanosensory signals and control the motor pattern of flight muscles. Second, lepidopteran, coleopteran, hymenopteran, and dipteran insects maintain a special relationship with flowering plants, which made way for further division of niches. Color vision, odor discrimination and pat-

tern recognition have become more sophisticated during the coevolution of these insects and flowering plants (e.g. Chittka and Menzel, 1992). Third, complete metamorphosis has allowed conspecific juveniles and adults to utilize different resources, thus reducing competition. To regulate metamorphosis, the development of an endocrine system and coordination with the nervous system were required.

While arthropods are the most successful group in terms of species richness and diversity, they are far less successful than higher vertebrates, especially mammals, in terms of complexity of the body structure and behavior. On the phylogenetic tree, arthropods and vertebrates are located at the top of the two major animal lineages, the protostomes and the deuterostomes, respectively (Fig. 1). These two groups attained evolutionary success by exploiting completely different life styles. Pianka (1970) argued that for short-lived animals with a small body size, such as insects, the reproductive strategy is to produce a large number of offspring at each reproduction; each offspring, however, has only a small prob-
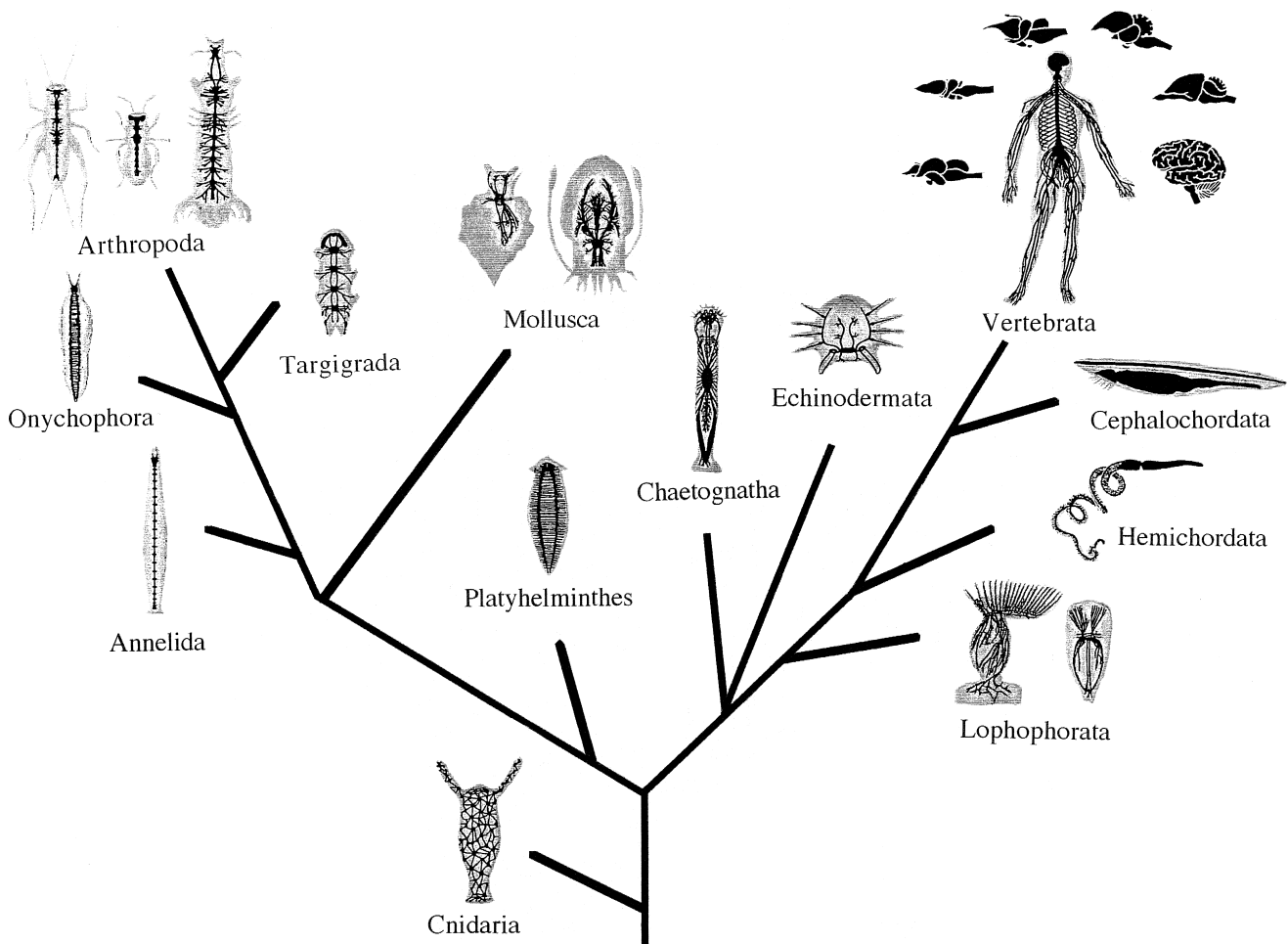
Fig. 1. Phylogenetic tree of the animal kingdom showing the evolution of nervous systems. The animal kingdom is divided into two branches, the protostomia and the deuterostomia. The most complicated physical structures and behavioral patterns are found among vertebrata, arthropoda, and mollusca. The nervous systems of arthropods share a number of features with higher vertebrates, reflecting convergent evolution, but also exhibit many specific features reflecting adaptation to their characteristic lifestyles. The dendrogram shown is based on Brusca and Brusca (1990).

Table 1. Some of the correlates of *r*- and *K*-seection. From Pianka (1970).

	r-Selection	*K*-Selection
Climate ·································	Variable and/or unpredictable: uncertain	Fairly constant and/or predictable: more certain
Mortality ·····························	Often catastrophic, nondirected, density-independent	More directed, density-dependent
Survivorship ························	Often Type III (Deevey 1947)	Usually Type I and II (Deevey 1947)
Population size ··················	Variable in time, nonequilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecologic vacuums; recolonization each year	Fairly constant in time, equilibrium; at or near carrying capacity of the environment; saturated communities; no recolonization necessary
Intra- and interspecific competition ····················	Variable, often lax	Usually keen
Relative abundance ···········	Often does not fit Mac Arthur's broken stick model (King 1964)	Frequently fits the Mac Arthur model (King 1964)
Selection favors ·················	1. Rapid development 2. Highr r_{max} 3. Early reproduction 4. Small body size 5. Semelparity: single reproduction	1. Slower development, greater competitive ability 2. Lower resource thresholds 3. Delayed reproduction 4. Larger body size 5. Iteroparity: repeated reproductions
Length of life ······················	Short, usually less than 1 year	Longer, usually more than 1 year
Leads to ·····························	Productivity	Efficiency

ability of survival to adulthood. For long-lived animals with a large body size, such as terrestrial vertebrates, the strategy is to produce a small number of offspring, each with a high chance of survival. The former species are referred to as relatively *r*-selected and the latter as *K*-selected (*K* refers to the carrying capacity of the environment at equilibrium and *r* to the maximal intrinsic rate of reproduction in the logistic formula). Table 1 shows some of correlates of *r*- and *K*-selections (Pianka, 1970). Animals with different reproductive strategies require different behavioral capabilities. For example, a high capability of dispersal is important for *r*-selected species, while *K*-selected animals require a high capability of learning since they typically adapt to environmental change by modifying individual behavior. In addition, small, *r*-selected animals utilizing microhabitats require relatively limited behavioral repertories compared to large, *K*-selected animals utilizing diverse environmental resources. Optimization to support life style of relatively *r*-selected animals is probably one of design principles of arthropod "microbrain".

ORGANIZATION OF THE ARTHROPOD MICROBRAIN

In Fig. 2, a generalized scheme of the central nervous system of an arthropod is illustrated, using the honey bee as an example. Serially arranged ganglia along the length of the body are connected by a pair of axonal commissures to form a rudder-like nervous system. Ganglia of the head are fused to form a brain and a subesophageal ganglion. The brain contains sensory, associative and premotor centers that include: the antennal lobe (olfactory center); the dorsal lobe (antennal mechanosensory center); the optic lobe (visual center); the mushroom body, which is critical to olfactory learning (Davis, 1996; Heisenberg, 1998), place learning (Mizunami *et al.*, 1998d), and higher motor control (Huber, 1960; Mizunami *et al.*, 1998c; Okada *et al.*, 1999); the central complex, which is implicated in motor coordination (Strauss and

Heisenberg, 1993); and the posterior slope and the lateral accessory lobe, which are premotor centers from which descending neurons originate to supply the thoracic ganglia. Signals from the brain are transmitted to motor circuits in thoracic or abdominal ganglia for execution of locomotory or other behavior.

FUNCTIONAL ADAPTATION OF THE ARTHROPOD MICROBRAIN

How can the basic design of the arthropod brain be understood in terms of functional adaptation and evolutionary constraints? We suggest that two factors, the smallness of the number of neurons and the optimization to the life style with a small body, are crucially related to the basic design of the arthropod brain.

a) Small number of neurons

The small body size of most arthropods has set a fundamental constraint on the design of their brain by limiting the number of its constituent neurons. Computation by means of a small number of neurons is, in essence, characterized by quickness, simplicity, and economy, whereas that by means of a large number of neurons is characterized by accuracy, complexity and flexibility. Economical and speed-oriented features of the arthropod "microbrain" are evident in that (1) the sensory systems of arthropods typically extract relatively small numbers of biologically significant features so that the need for further central processing is reduced (Wehner, 1987), (2) learning in arthropods is, typically, a modification of a specific element of stereotyped behavior (Alcock, 1989; Menzel, 1990; Wehner, 1992) and (3) most arthropod behavior is controlled by motor command systems that consist of a relatively small number of neurons and produce quick and relatively stereotyped motor patterns (Wiersma and Ikeda, 1964; Liebenthal *et al.*, 1994; Kolton and Camhi, 1995; Sparks *et al.*, 1997). It
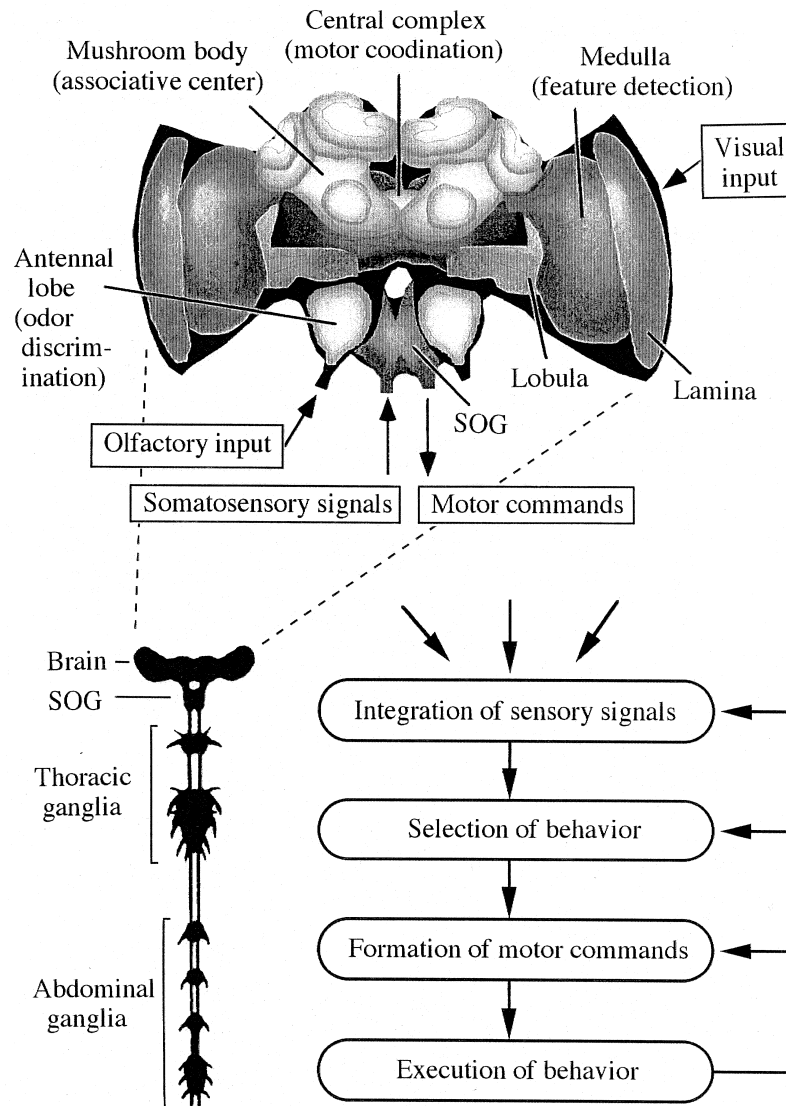
Fig. 2. A schematic illustration of the organization of the central nervous system of the honey bee, based on Mobbs (1985). The central nervous system consists of the supraesophageal, subesophageal, thoracic, and abdominal ganglia. The supraesophageal ganglion (brain) contains sensory, associative and premotor centers, including the optic lobe (the visual center that consists of three neuropils; i.e., the lamina, medulla, and lobula), the antennal lobe (olfactory center), the mushroom body (associative center), the central complex (a center for motor coordination), and the posterior slope and the lateral accessory lobe (premotor centers from which descending neurons originate). Signals from the brain are transmitted to the thoracic ganglia for execution of locomotory behavior. Thoracic ganglia contain motor circuits for locomotion. The subesophageal ganglion (SOG) contains a center for feeding. Abdominal ganglia contain centers for digestion, excretion and copulation.

can be pointed out that the third point (3) is in accord with the functional need of small animals, since quickness is a major requirement for controlling motion of small animals because the time-scale of motion of smaller animals tends to be smaller due to smaller mass of inertia.

An example of adaptive specialization of the arthropod nervous system is discussed below. The motor systems of crustaceans and insects contain a number of non-spiking premotor interneurons that transmit signals by way of graded, not action potentials (Takahata and Hisada, 1991). Non-spiking interneurons have never been found in the motor systems of vertebrates. Each part of these interneurons can act as an independent processing unit and, thus, a single neuron can

act as a multi-processor (Hikosaka and Takahata, 1998). Non-spiking interneurons are also able to operate as the integrating processor of various sensory and central inputs to allow for switching between different motor patterns or to form smooth motor responses (Takahata and Hisada, 1991). The versatility of non-spiking neurons is a good example of adaptation to attain an enhanced signal processing capability with a limited number of neurons.

The mushroom body of the insect brain provides a curious exception to the general rule that a relatively small number of neurons serve as the basic processing unit in the arthropod brain. In the cockroach, each mushroom body contains 200,000 intrinsic neurons (Neder 1959) that are orga-

nized into ca. 15 repetitive modular subunits, each subunit consisting of a pair of slabs (Mizunami *et al.*, 1998a, b). It is likely that slabs act as functional units (Mizunami *et al.* 1998a, Iwasaki *et al.* 1999). Computation in each slab may be based on the synergistic operation of a large number of neurons, as is typical in the mammalian cortex (Georgopoulos *et al.*, 1986, 1988).

b) Adaptation to life with a small body

Small terrestrial arthropods that utilize microhabitats are threatened by changes in the environment. This is related to the physical rule that the smaller a given animal is, the higher is the surface-to-volume ratio and, thus, the more susceptible it is to environmental change. For this reason, terrestrial arthropods developed the ability to detect minute changes in temperature, humidity and carbon dioxide concentration. Here, we focus on humidity detection by insects. Cockroaches, honey bees and many other insects have hygroreceptors on their antennae. The response of hygroreceptors depends on relative humidity, and the mechanism of the primary process of hygroreception is non-chemical (Yokohari and Tateda, 1976; Yokohari, 1978). There is evidence to suggest that the hygroreceptors transduce humidity changes to electrical potential through mechanical strain induced in hygroscopic components of the sensillum (Yokohari, 1978, 1981). Thus, insects probably developed their hygroreceptors through modifying mechanoreceptors. In accord with this theory, axon terminals of hygroreceptors occupy the dorsal margin of the antennal lobe, an area adjacent to the dorsal lobe in which axons of antennal mechanoreceptors terminate (Nishikawa *et al.,* 1995).

It has been argued that small, short-lived animals are capable of responding to environmental change by genetic change (Pianka, 1970; Johnston, 1982), hence, the ability to learn from experience is relatively unimportant. Recent studies, however, showed that even one of the smallest and shortest-lived insects, the fruit-fly *Drosophila*, can perform various forms of olfactory, visual and motor learning (Davis, 1996, Wolf *et al.*, 1998). Thus, learning is probably a more essential element of arthropod behavior than it has hitherto been considered. Mayr (1974) argued that the social or communicative behavior of animals tends to be relatively inflexible, while resource-directed behavior is more likely to be flexible because the environment is so variable. This argument is, no doubt, applicable to arthropods. Some of the fascinating resource-oriented behavior of arthropods that include memory-dependent components are: the mass migration of spiny lobsters on the basis of magnetic orientation (Lohmann *et al.*, 1995); the homing by motor memory of fiddler crabs (Hagen, 1967), wandering spiders (Seyfarth *et al.*, 1982) and orb-weaving spiders (Mittelstaedt, 1985); sun or skylight compass orientation of bees and ants (Wehner, 1989, 1992; Wehner *et al.*, 1996); the foraging behavior of honey bees that is dependent upon the ability to learn about the odor, color, shape, and location of food sources (Frisch, 1967; Gould and Gould, 1988; Menzel, 1990; Chittka and Menzel, 1992, Srinivasan *et al.*,

1998); and the communication between honey bees of information concerning the distance and direction to food sources by a waggling dance (Frisch, 1967). The brain mechanisms underlying these types of behavior remain for subjects of future investigations.

DIVERSITY AMONG ARTHROPOD MICROBRAINS

There are notable variations in the organization of brains among different arthropod groups. Scorpions have olfactory sensilla on abdominal appendages (Gaffin and Brownell, 1997) and these appendages are not homologous to insect antennae. Interestingly, axon terminals of scorpion olfactory sensilla form glomeruli in thoracic neuromeres (Brownell, 1991), just as axons of insect olfactory sensilla form glomeruli in the antennal lobe. In the crustacean brain, neuropil homologous to the insect mushroom body has not been identified (Strausfeld, 1998). Further, the central body of spiders is probably not homologous to the central complex of insects (Breidbach, 1995); i.e., the central body in spiders appears to be a visual center (Strausfeld *et al.*, 1993), whereas the central complex of insects plays a role in motor coordination (Strauss and Heisenberg, 1993). The structures of first and second neuropils in the optic lobe of insects are in large part homologous to that of crustaceans, but the third optic neuropils may have evolved independently in each group (Strausfeld, 1998). How these varied features among arthropods are related to evolutionary history and functional adaptations remains to be elucidated.

COMMON FEATURES OF THE ARTHROPOD MICRO-BRAIN AND THE MAMMALIAN MEGALOBRAIN

Although we emphasize that the "microbrain" of arthropods is optimized to their specific lifestyle, it is also evident that the arthropod "microbrain" shares many features with the mammalian "megalobrain". For example, the primary olfactory center of insects (antennal lobe) has many structural and functional similarities to that of mammals (olfactory bulb) (Laurent *et al.*, 1996; Hildebrand and Shepherd, 1997). Signal processing in the visual system of insects also shares various features to that of mammals (Laughlin, 1981; Hengstenberg, 1991; Strausfeld and Lee, 1991; Land, 1992; O'Carroll, 1993); for example, the computational algorithm for motion detection in insects is the same as that in humans (Adelson and Bergen, 1985; Reichardt, 1987). Olfactory and visual learning in honey bees has features similar to those in mammals (Bitterman and Couvillon, 1991; Bitterman, 1996). The motor systems of arthropods share many features with those of mammals (Camhi, 1993; Pearson, 1993; Selverston *et al.*, 1997; Sparks *et al.*, 1997). Since the brains of arthropods and mammals have been evolved independently from the less-organized head ganglia of common flatworm-like ancestors (Willmer, 1990), these similarities are the result of convergent evolution. Functional convergence among different animal lineages is not surprising considering the similarity of physical

environments in which animals survive and of the biological tasks in which animals engage; i.e., finding a habitat, searching for food, avoiding predation, finding a mate, and adapting behavior in response to internal and external environmental changes.

Many fundamental similarities have been found in molecular and cellular mechanisms underlying brain functions among insects and mammals. Examples of these similarities are (1) the presence of homeotic genes that determine the morphology of the body and body parts (Carroll, 1995), (2) the common cellular process for the development of the nervous system (Murphey, 1986), and (3) common molecular basis for learning and memory (Kandel and Abel, 1995; Davis, 1996). Most of these appear to be successional from common ancestors. Arthropod brains are highly accessible to detailed experimental examination and provide useful model systems for the study of common mechanisms underlying brain functions.

CONCLUDING REMARK

One ultimate goal of neurobiology is to elucidate the diversity and evolution of brains throughout the animal kingdom, and elucidation of the arthropod brain will be an important step for achieving this goal. Many unanswered questions remain in this broad field of research. For example, how can the brains of molluscs, which include the most sophisticated brains of all invertebrates (i.e., that of the octopus), be characterized in comparison to the arthropod microbrain and mammalian megalobrain? Elucidation of diversity among animal brains will lead to a deeper understanding of principles related to their design, including those of the human brain.

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