Norwegian University of Life Sciences

Dept. of Animal and Aquacultural Sciences

SENTIENCE AND PAIN IN INVERTEBRATES

Report to Norwegian Scientific Committee for Food Safety

Av

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FINAL REPORT

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CONTENT

BACKGROUND AND DESCRIPTION OF THE TASK

The Norwegian Scientific Committee for Food Safety was asked by The Norwegian Food Safety Authority to produce a report on risk assessment of the ability of various groups of invertebrates to sense and perceive discomfort, pain and stress. Department of Animal and Aquacultural Sciences at the Norwegian University of Life Sciences accepted to produce a report on the topic as a background for the risk assessment. Professor emeritus Lauritz Sømme from Department of Biology at University of Oslo, a well-known invertebrate zoologist, accepted to produce the body of this report.

This report briefly describes the sensory and neural systems of the following invertebrate groups: Mollusca, Echinodermata, Annelida, Insecta, Arachnida, and Crustacea. In addition, cognitive abilities and the neurobiological potential for pain and suffering are presented to the extent this is known from scientific literature. The report ends with a concluding chapter summarizing the findings and discussing the extent to which sentience and pain can be found in the various invertebrate groups. As will be evident from the text, conclusions must be drawn quite cautiously.

The main concern of the Animal Welfare Act is situations in which humans influence animals. Direct research on this is virtually non-existent in invertebrates. Conclusions relevant for animal welfare legislation must therefore be based on the more general scientific knowledge.

INTRODUCTION

Invertebrates are animals without backbone. At present approximately 1.3 million species have been described, and new species are regularly discovered. In comparison, 46 700 species of vertebrates are known (Brusca & Brusca 2002). Invertebrates include many groups or phyla with small, soft and wormlike bodies, while in other phyla the body is covered by a hard cuticle or shell. Invertebrates appear in astronomical numbers of individuals and are basic factors in marine, freshwater and terrestrial ecosystems.

The ability of animals to avoid dangers or aversive stimuli is part of their adaptation to the environment. Avoidance of mechanical damage, heat, cold, chemicals and other environmental factors is a necessity for survival. Invertebrates are well equipped with sense organs, which supply information about their surroundings. Like vertebrates, invertebrates respond to noxious stimuli by withdrawal in order to reduce the likelihood of damage. The response can be fast reflexes or more graded neural responses.

Humans often treat invertebrates as if they are without feeling. A number of invertebrates are caught and handled for consumption, e.g. crayfish, lobster, crabs, shrimps, insects, snails and cephalopods [In Norwegian: ferskvannskreps, hummer, krabber, reker, insekter, snegler og blekkspruter]. Many species are cultivated for sale in large quantities. Furthermore, invertebrates are widely used for experimental purposes, including toxicological research and pest control. Since it is assumed that they cannot feel any pain, or at least are less sentient than vertebrates, it is suggested that invertebrates whenever possible should replace vertebrates in biomedical research.

The different attitude to vertebrates and invertebrates is reflected in the legislation of animal welfare of most countries. In Norway, crustaceans [krepsdyr] only are included in the animal welfare act, and the regulations restrict this group to decapods [tifotkreps].

Since pain and suffering are “personal” experiences, it is not possible to know what animals are feeling. Compared to vertebrates, research on cognition and sentience in invertebrates has to be based on more indirect methods on their behaviour as well as neural morphology and capacity. Unfortunately, there is a paucity of results in this field. The purpose of the present report is to discuss what is known about the occurrence of sentience and pain in invertebrates.

EVOLUTION OF THE ANIMAL KINGDOM

The animal kingdom originated in the Precambrian more than 700 million years ago. The fossil records from this era are scanty but the subsequent evolution of diversity in the Cambrian has been described as explosive (Dorit et al. 1991, Brusca & Brusca 2002). Most of the fossil records of animals extend from 570 millions years ago till present, and surprisingly almost all of our present day major groups or phyla were present in the Cambrian. In addition, the Cambrian fauna included phyla which later became extinct. In the Cambrian, all animals lived in the ocean, and terrestrial animals did not appear until the Devonian period, about 350 million years ago.

At an early stage, the animal kingdom, with the exception of some minor phyla, were divided into two branches, separated by features of their embryological development. In the deuterostomes the cleavage of the embryo is radial and the mouth arises as a new opening at the end of the embryo. The protostomes exhibit a spiral cleavage and the mouth arises from the original invagination in the blastopore of the embryo. Humans and all other vertebrate animals belong to the deuterostomes. The only deuterostome invertebrate animals included in the present report are the echinoderms [pigghuder].

Most invertebrate animals belong to the protostome branch of the evolutionary tree. In this branch we find annelid worms, molluscs, crustaceans and insects [leddormer, bløtdyr, krepsdyr og insekter]. While the molluscs, including gastropods, bivalves and cephalopods [snegler, muslinger og blekkspruter], formed a side branch at an early stage, the arthropods [leddyr], including crustaceans, insects and spiders [edderkopper], formed the most diversified groups of the animal kingdom. They clearly originated from annelid worms, as appear from similarities in the nervous system and segmentation of their bodies.

The separation of vertebrates from most of the invertebrates at an early stage in the evolution of the animal kingdom, suggests that fundamental differences in the central nervous system and sense organs may have evolved.

CENTRAL NERVOUS SYSTEM OF VERTEBRATES

Morphology

For comparison and a better understanding of the great differences between the central nervous systems of vertebrates and invertebrates, a short description of the vertebrate system is presented, based on the textbook of Dorit et al. (1991) and other sources.

In humans, our feelings are related to the cerebral cortex. The cortex includes large sensory and motor area, but most of it is occupied by association areas. The forebrain of humans is divided into a telencephalon and diencephalons. The telencephalon includes the olfactory bulbs and the cerebrum with the cerebral cortex. The telencephalon represents a dominant part of the nervous system in the evolution of the vertebrate brain. The cerebrum is relatively small in primitive vertebrates but has been greatly enlarged during evolution and became the dominant part of the brain in mammals.

The midbrain (mesencephalon) forms a pair of large optical lobes in fishes, amphibians and reptiles. The hindbrain (metencephalon) includes the cerebellum, which is an important center for motor coordination. Cerebellum is particularly large in fishes, in particular in highly active species, and in birds and mammals as well.

The olfactory bulbs occupy a relatively large part of the brain in fishes, amphibians and reptiles. The cerebrum is quite small in fishes, but slightly larger in amphibians and reptiles. In birds the cerebrum is a dominant part of the brain, and even more in mammals. In mammals increasing sizes of the cerebrum is found from primitive species, like shrews, and up to humans. In humans the cerebral cortex is composed of 100 billion neurons.

The increase in size of the cortex is accompanied by better memory, learning ability and consciousness. Part of human consciousness is sentience, pain and fear. These feelings or emotions may be present in most vertebrates, and increase in magnitude with the cerebral cortex. When the nervous system of a species attains a sufficient level of complexity during evolution, it is believed that some state of consciousness will appear (Chandroo et al. 2004).

Fishes possess the smallest brain and cerebral cortex among the vertebrates, and their nervous system is interesting for comparisons with invertebrates.

In conclusion, most four-legged vertebrates have some state of consciousness, while this is uncertain in fish. In the present report the complexity of the nervous system of invertebrates is described, bearing in mind how the central nervous system of vertebrates has been developed. The question is if invertebrate species with relatively complex brains may be aware of their surroundings and perhaps feel pain and stress.

Electrical activities

In addition to morphological differences, the electrical activities from the brains of invertebrates differ from those of vertebrates and of some cephalopods (Bullock 1984). In vertebrates, the activity is dominated by slow components in the range of 0 to 30 Hz, and fast events, such as spikes (action potentials), are seen by special stimuli. In contrast, electrical activity from the brains of invertebrates like crayfish, earthworms, snails and grasshoppers is dominated by spikes with relatively weak components from around 5 Hz to 50 Hz. The difference in brain signals between vertebrates and invertebrates may depend on different anatomical arrangements of neurons and their processes.

In studies on the electric activity of the brain of the crayfish *Procambarus clarkii*, Ramon et al. (2003) found responses to stimuli with certain resemblance to those of vertebrates. So-called event-related potentials found in the crayfish are known from studies on humans. In humans they are considered to be signs of higher stages of processing, and sometimes referred to as cognitive waves. Other responses of the crayfish brain also resemble those of the brains of mammals. The results does not imply that crayfishes are capable of elaborate mental operations, but at least that some simple nervous mechanisms of basic importance for cognition is present. New results like these should be considered when evaluating the possibility of sentience in invertebrates.

NERVOUS SYSTEMS AND SENSES IN INVERTEBRATES

Echinodermata

The echinoderms include approximately 7 000 species, of which sea stars, sea urchins and sea cucumbers [sjøstjerner, sjøpiggsvin og sjøpølser] are best known. At least some species of the latter two groups are handled for human consumption. The ovaries of sea urchins are considered a delicacy in many countries, and dried slices of sea cucumbers are popular in many Asian countries.

Although the echinoderms are closer to humans and other vertebrates on the phylogenetic trees than any other invertebrates, their nervous system is quite simple. This may be a result of a secondary development of radial symmetry from ancestors with bilateral symmetry (Brusca & Brusca 2003). Typical representatives like sea star and sea urchins have a five-parted radial symmetry. Their nervous systems include an integrated network of nerves, but lack a cerebral ganglion. An important part of the system is a nerve ring that encircles the mouth, and five radial nerves that extend from the ring into different parts of the body. The nerves control the coordination of movement in the unique water vascular system. If the main radial nerve is cut, however, the row of suckers may still continue to move independently.

Sensory receptors are located in the epidermis, and innervated by the nervous network. They are concentrated along the row of tubular feet or connected to spines and other outgrowth of the body. The receptors are sensible to touch, chemicals, water currents and sometimes light, while some species also have special photoreceptors. Chemoreceptors apparently react more to contact than to distant input.

In spite of their relatively simple nervous system, the echinoderms show complex behavioral patterns. They are able to turn over if placed on the back, and can orient themselves to currents in the water. In conclusion, these slow moving animals are able to survive even without a complicated nerve system, but their survival also depends on the protection offered by their stiff and spiny bodies.

Segmented worms – Annelida

Diversity

The segmented annelid worms comprise approximately 17 000 species (Brusca & Brusca 2003). They occur in all moist habitats, and are particularly abundant in the sea and in fresh water. The anatomy of annelids is relatively simple. Their elongate, segmented body is usually cylindrical, but flattened in some species.

The annelids are divided into three groups. Polychaetes [flerbørstemark] are mainly marine animals. They have numerous bristles and prominent parapodes at the side of the body. The oligochaetes [fåbørstemark], which include earthworms [meitemark], have a smoother surface and fewer bristles. In the leaches [igler] (Hirudinea) the body is flattened.

Several species of annelids are handled by humans. In relation to animal welfare it is reasonable to ask if earthworms feel pain when used as bait and wriggle on the hook.

Marine polychaeta, like sandworms, are also used for bait. Bloodsucking leaches are still cultivated and used in medicine.

Central nervous system

The central nervous system of annelids includes a dorsal cerebral ganglion, paired connectives around the gut and one or more ventral nerve cords. The same fundamental plan is also found in arthropods; e.g. see illustration of an insect (Figure 5).

The cerebral ganglia of the polychaetes are bilobed, and more primitive forms have two longitudinal ventral nerves with pairs of ganglia in each body segment. In the oligochaetes, the brain is more compact, and the ventral nerve cords are fused to a single string with ganglia. The cerebral ganglion is often divided into three regions; the forebrain, midbrain and hindbrain. The different parts innervate different sense organs at the head and along the body. In comparison, the division of the brain is more pronounced in arthropods.

Sense organs

Polychaete annelids possess an impressive array of sensory receptors (Brusca & Brusca 2003), but the numbers vary greatly among species with different lifestyles. The polychaetes are highly sensitive to touch. Mechanoreceptors are distributed over much of the body surface and concentrated in the head and parapodia.

Most polychaetes have photoreceptors that give information on light intensity and direction of light, but complex eyes are lacking. Chemoreceptors are scattered over the body, and polychaetes are sensitive to dissolved chemicals. They are sometimes useful as indicators of pollution.

The sense organs of oligochaetes consist of various types of epithelial organs distributed over most of the body. The receptors can be free nerve endings within the epidermis, or clusters of special receptor cells. The functions of all cell types are not known. Some are apparently tactile organs, and some are chemoreceptors.

Leaches also possess an array of sense organs, similar to those of oligochaetes. Leaches have up to ten simple eyes, and bloodsucking species react positively to light when preparing to feed. They are also attracted by increased temperatures, e.g. by a human leg in the water.

In conclusion, annelid worms represent a highly diversified group of animals. They register their surroundings through numerous sense organs, but have relatively simple central nervous systems.

Molluscs

Diversity

Molluscs include some primitive forms like Aplacophora and Polyplacophora (chitons), as well as Gastropoda (snails and slugs), Bivalvia (bivalves or clams) and Cephalopoda (squids, octopuses, etc.). The molluscs are highly diversified and include more than 93 000 species. Several species are caught or handled by humans, e.g. oysters and mussels that are cultivated in large quantities. Other clams and shells are collected for consumption. In France the sales of collected and farmed vineyard snails (*Helix*) amount to 50 millions Euro per year. A variety of marine species, including the big sea hare (*Aplysia*), are eaten in Asia. In Norway, the small *Littorina* species of the intertidal zone may be consumed. Cephalopods, like squids and octopuses, are caught in large quantities both for human consumption and for bait.

The basic plan of the nervous system is found in chitons and other primitive molluscs, and in more specialized forms in more advanced molluscs.

Aplacophorans

Chitons and the worm-like aplacophorans have very simple nervous systems (Brusca & Brusca 2003). They consist of two pairs of nerve cords with small ganglia in the head region, and sometimes with ganglia at the rear end of their bodies (Figure 1A). The nerve cords are connected by transverse commissures.

Bivalves

In the bivalves or clams, the central nervous system includes two pairs of nerve cords. Due to fusions there are only three pairs of ganglia (Brusca & Brusca 2003). From the brain-like ganglia behind the mouth, two nerve cords lead to visceral ganglia at the rear end and to the pedal ganglia in the foot. Although the ganglia are quite large in size, the nervous system of the molluscs is relatively simple (Figure 1B). Their nervous system is not sufficiently complex to deal with sensations, and it is unlikely that they have any feelings or sentience.

Sensory organs of molluscs are mainly found along the edge of the mantle. They include both tactile receptors and chemoreceptors. Statocysts are often present in the foot of burrowing bivalves, and simple eyes along the mantle edge. The eyes of the swimming clam *Pecten* are actually supplied with lenses. In general, it appears that molluscs are well equipped with sense organs to register their surroundings.

Gastropods

Central nervous system

The gastropods are a highly diversified group. Traditionally, the group is divided into prosobranchs [forgjellesnegl] with gills in their front end, opistobranchs [bakgjellesnegl] with gills in the rear end, and pulmonates [lungesnegl]. The latter includes freshwater and land snails.

The ganglia of the central nervous system in various groups of gastropods are arranged in a number of different ways (Chase 2002). The gastropod nervous system has been characterized as a most difficult problem in comparative anatomy, and it is almost impossible to give a general description.

Generally, the central nervous system includes pairs of buccal ganglia, cerebral ganglia and pedal ganglia. In addition, there are often two visceral ganglia. In some species there are also two intestinal ganglia. The paired ganglia may be linked by commissures, and some of them are linked by long connective nerves. Due to torsions during formation of their spiral shells, the nervous system of some gastropods attains the shape of the figure eight (Figure 1C).

Each ganglion is surrounded by a sheath that confines the nervous system and glia cells. The ganglia, neurons and glia cells form an outer cortex, while the central core is mainly composed of neuropil and fiber tracts.

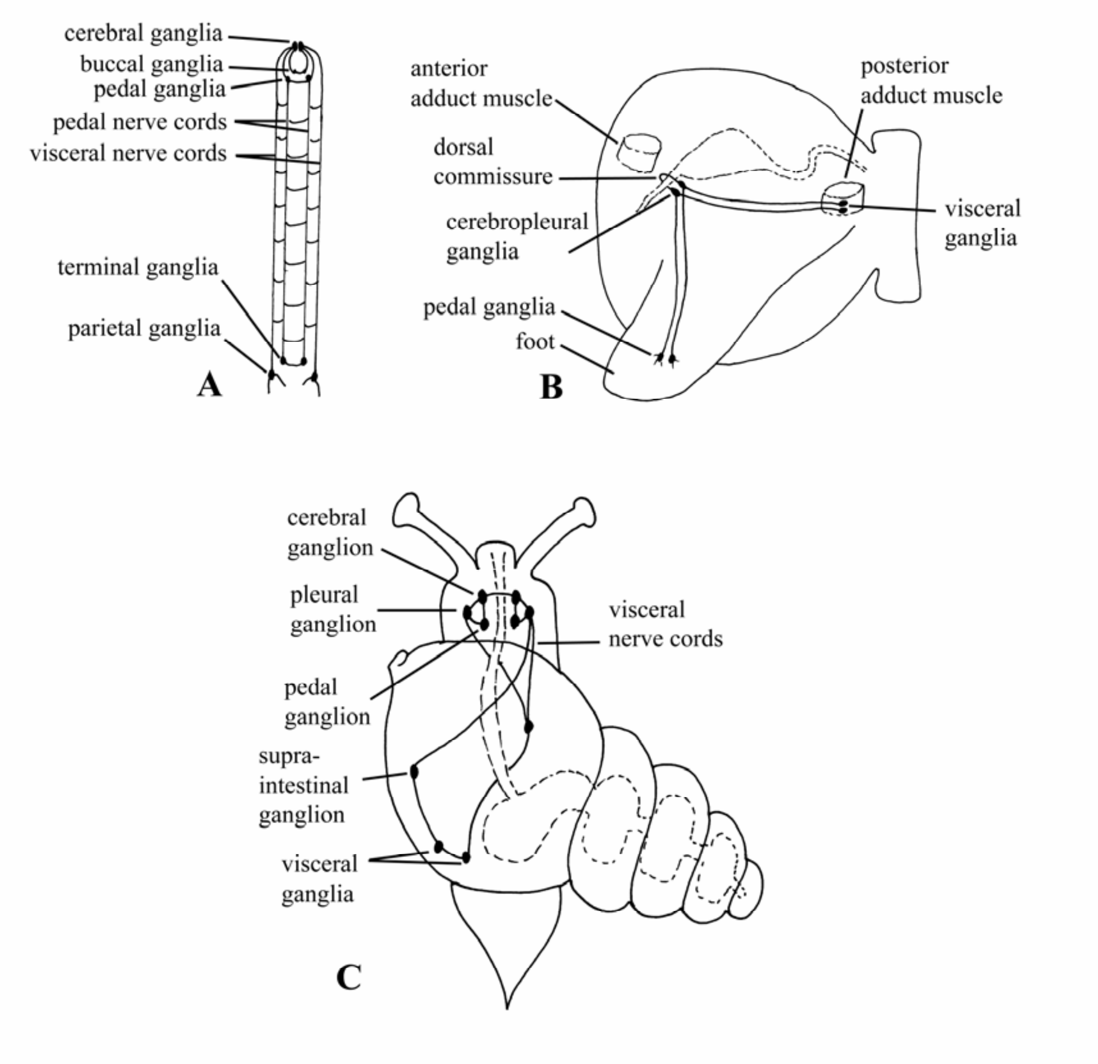

Figure 1. The central nervous system of molluscs. A. Aplacophora, B. Bivalvia (clam), C. Gastropoda (snail).

Some properties of the gastropod nervous system have been of importance for understanding the function of the nervous system in other animals. Most species of opistobranchs and pulmonates contain giant neurons. A neural cell body of 1000 µm in diameter in *Aplysia* is the largest known neural cell in any animal. For this reason, *Aplysia* has been widely used in neurobiological research on e.g. learning mechanisms. Like in most crustaceans, but unlike vertebrate neurons, gastropod neurons are seldom bipolar. A single process combines axonal and dendritic functions.

Sense organs

In the world of snails and slugs there are no sounds, and in most cases no sights (Chase 2002). Some gastropods have eyes, but mostly for registration of the presence of light. Only few species have eyes that can be used for recognition of objects. Thus, perception of the external world usually depends on a combination of chemoreception and mechanoreception. These sense organs are also the most important regarding the question of handling and cultivating gastropods. In addition, gastropods have proprioceptive sense organs, to inform about the positions of the body, and are able to sense gravity due to the presence of statocysts.

Sense organs of snails and slugs are difficult to study, but apparently chemoreceptors are the most numerous. Two types of chemoreceptor cells have been distinguished. Some are specialized for identification of close objects, while others are specialized to “smell” chemicals from more distant origin. Chemoreceptors are found in various parts of the body, but are often concentrated around the mouth, in the foot and at the tentacles. A special type of chemoreceptors is situated in the mantle cavity of many species. The function of these receptors is probably to register the quality of the water that passes over the gills.

Mechanoreceptors are spread out all over the skin of gastropods. They are important in locating food, finding a partner and for defense purposes. Several types of mechanoreceptors with sensory endings in the epithelial surface have been described.

Some sensory cells are especially responsible to noxious stimuli (Chase 2002). This includes both mechanical and chemical stimuli. The cells resemble nociceptors which are more typical of vertebrates. Morphologically, the nociceptive receptors cannot be distinguished from ordinary mechanoreceptors, but some have been identified by physiological properties. In this way clusters of receptors in *Aplysia* have been identified as nociceptors.

Learning in gastropods

Learning has been defined as a process which manifests itself by adaptive changes in individual behaviour as a result of experience (Nixon & Young 2002). Gastropods may exhibit several types of simple learning. The repetition of stimuli typically leads to a progressive diminution of the response (Chase 2002). This is known as habituation, and depends on a single type of stimulus to modify the behaviour. General sensitization is another form of non-associative learning, and involves physiological changes for defensive behaviour. Examples of simple associative learning (one stimulus predicts another, classical conditioning) are described in the sea hare *Aplysia* and in the garden snail *Helix*. The neurobiological mechanisms of these learning types are well understood in Aplysia (Hawkins et al. 1983), although the exact ways the short-term memory are converted to long-term memory are still unknown.

Cephalopods

Central nervous system

Among the invertebrates the most complicated nervous system is found in some of the cephalopods, which includes *Nautilu*s, octopuses with eight arms, and other species with ten arms or tentacles e.g. *Todarodes saggitatus* [akkar]. The advanced nervous system is related to their way of life. Cephalopods are predatory animals that are highly active and mobile. In all species the nervous tissues form a compact brain surrounding the gut (Nixon & Young 2003). The greatest concentration is found in species with eight arms, while the brain is less concentrated in nautilids and species with ten arms. The central nervous system of cephalopods includes many of the ganglia found in other molluscs. Examples are the paired cerebral, buccal, labial, pedal, brachial, optic, olfactory and peduncle ganglia. Since they are concentrated into a compact mass, the ganglia are not easily distinguished, but appear more as part of lobes.

Even *Nautilus,* which is the only presently living cephalopod with an external shell, has a more complex brain than any non-cephalopod mollusc. A total of thirteen lobes are discernable. The more complicated brain of *Octopus* (Figure 2) and other species with eight arms comprise masses of nervous tissue above and below the oesophagus of the gut, and are divided into 25 major lobes. In general, the brain and its lobes are relatively smaller in species with ten arms. In the octopuses the parts above the oesophagus are the most complicated, and characterized as the highest centers of the brain. It includes the buccal ganglia, which are motor centers for the control of feeding, and receives inputs from the eyes and the arms.

As pointed out by Nixon & Young (2003) in their comprehensive textbook on cephalopods, the brain to body ratio exceeds that of most fishes and reptiles. In the *Octopus vulgaris* the brain continues to grow during the lifetime, and the number of neural cells increases to about 200 millions. More than half of the cells are located in the optic lobe, which is connected to the highly advanced eyes of the octopus. Still, a brain of this size is of particular interest for considering consciousness in invertebrates, as will be discussed below.

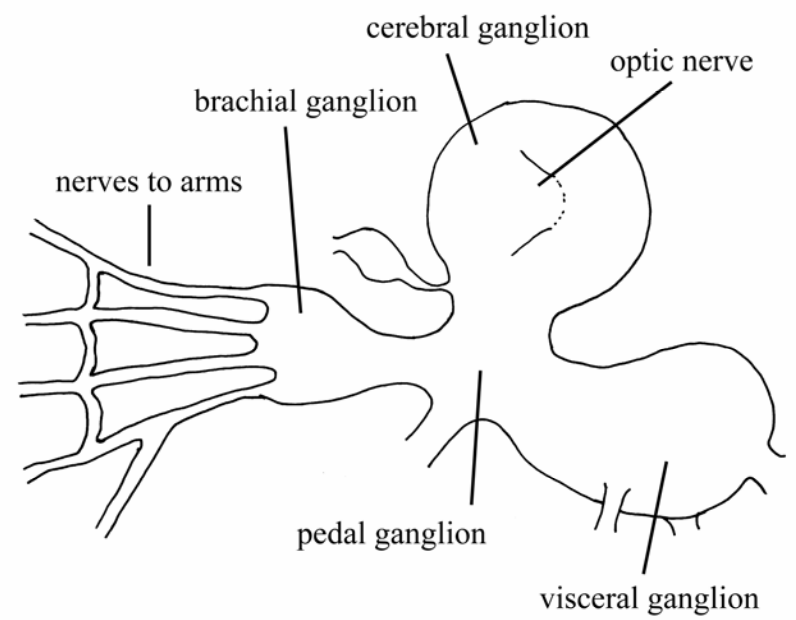

Figure 2. The enlarged and compact brain of *Octopus* (Cephalopoda). The ganglia correspond to similar ganglia in other molluscs (see Figure 1).

<u>Sense organs</u>

The eye of *Nautilus* is only a simple pinhole eye, but the eyes of most other cephalopods possess a lens (Nixon & Young 2002, Brusca & Brusca 2003). The eyes are superficially similar to those of vertebrates, and the two types have been considered as an example of convergent evolution. Although the cornea, iris and lens are arranged similarly to those of vertebrates, there are some principle differences, probably reflecting the fact that the two groups represent very different lines of evolution. Unlike the eyes of vertebrates, the cornea of cephalopods apparently contributes little to focusing. The retina in cephalopods comprises closely packed photoreceptors whose sensory end points towards the front of the eye. In this respect they differ from the indirect type of vertebrates. The retina of *Octopus vulgaris* contains 20 million receptor cells. The eye produces a perfect image. Behavioural studies have shown that *Octopus* can discriminate between forms, and that the eyes are important in supplying a wide range of information about the surroundings.

Both *Nautilus* and other cephalopods have statocysts that provide information that function as gravity receptor organs and detect rotary movements of the body. The statocysts of ten-armed cephalopods form the most complex equilibrium receptor system of all invertebrates and have a level of sophistication that is equivalent to that of the vestibular system of vertebrates. The arms of cephalopods are well equipped with tactile receptors, and mechanoreceptors are also found in other parts of the body. Some receptors are sensitive to local water movements, and are able to detect movements of fishes from a distance of 30 m. Chemoreceptors include both olfactory organs and contact receptors. Each sucker of the arms may contain several thousand chemoreceptors.

In conclusion, the cephalopods are well equipped with sense organs, some of which are the most advanced in the animal kingdom.

Learning in *Octopus*

Learning has been demonstrated in several species of cephalopods, but has been most closely studied in *Octopus vulgaris*. With their learning ability and behavioural flexibility they possess a high level of cognitive capacity (Mather 2001).

Under experimental conditions *Octopus* has been trained to take one kind of object, when awarded with food, and to reject other objects because small electrical shocks were given (operant conditioning). This training regime set up a memory that lasted for several days. Memory is important to an animal in its response to complex environments, and in the ability to identify objects and features in its surroundings. The memory system of *Octopus* is connected to certain lobes in the brain, and is capable of setting up memories both for vision and touch. Octopuses have visual abilities comparable to those of vertebrates. When blinded by cutting the optic nerves, they can be trained to accept certain objects by touch. Field observations have demonstrated that hunting by *Octopus vulgaris* mainly depends on the chemoreceptors, but that it has a spatial memory that makes it possible to use certain landmarks when foraging.

Crustaceans

Diversity

Crustaceans are one of the largest phyla in the animal kingdom, and include a large number of species. They are dominant animals in freshwater and marine ecosystems. Examples are krill and decapods that are most important as food for other marine animals. A number of crustaceans are parasites. Among the crustaceans the decapods are of particular interest regarding treatment of laboratory animals and animal welfare in general. The decapods are widely used as food for humans all over the world. Crayfish, lobsters and crabs are among species that are caught commercially or for private consumption.

Lobsters and crabs are often kept alive for long periods before being submerged in boiling water. It is reasonable to ask if the animals have any consciousness of this handling and will experience the treatment as painful. Crayfishes and shrimps are also boiled alive.

Several species of decapods are cultivated in large quantities for commercial purposes. They represent both an important source of proteins in some parts of the world, as well as delicacies. In Norway the cultivation of lobsters and crayfish is so far conducted on a small scale. Regardless of quantities, handling of decapod crustaceans should be carried out as careful as possible.

Central nervous system

The anatomy of the nervous system in crustaceans is as varied as the body forms of the group itself (Sandeman 1982). In more primitive species the central nervous system is like a ladder, similar to the system in annelid worms (Figure 3A). During embryological development pairs of ganglia are formed in each segment, joined across the midline by commissures and longitudinally by connectives. Ganglia can be described as groups or concentration of nerve cells, almost like small brains. The innervations from the ganglia of various parts of the body in crustaceans are well known.

Anteriorly, three pairs of ganglia are fused to form a brain. This varies considerably in size among the different taxonomic groups of crustaceans. The brain is the center of motor nerves to muscles in the head, and sensory neurons from the antennae and eyes.

As in annelids and other arthropods, the brain in crustaceans is situated above the esophagus, and linked to the ventral nerve cord by two connectives passing around the gut. In many species, the first ganglion of the ventral nerve cord, the subeosophagial ganglion, is relatively large. Nerves from the subeosophagial ganglion lead to muscles in the mouthparts from their sensory organs.

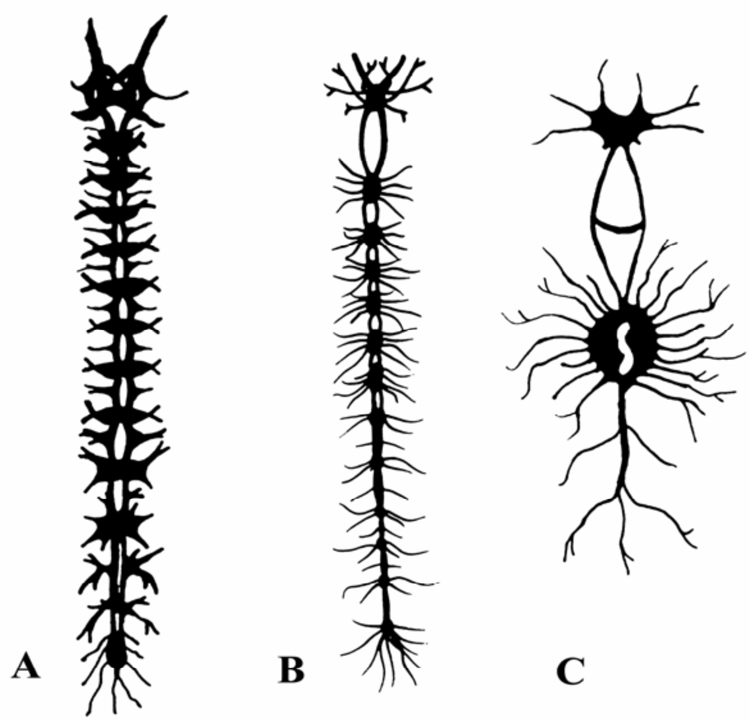

Figure 3. Central nervous systems in crustaceans. A. Ladder-like system of *Gammarus*. B. From lobster (*Homarus*) with fused ganglia in the ventral nerve cord. C. Highly compacted system of a crab (*Carcinus*).

In more advanced forms of crustaceans, e.g. lobsters, crayfish and shrimps, the ganglia of the ventral nerve cord are fused along the entire length of the body (Figure 3B). In short-bodied decapods, e.g. crabs, all thoracic ganglia are fused into one single mass (Figure 3C). As the abdomen itself, the abdominal ganglia are greatly reduced. An intermediate form is found in the spiny lobsters (*Panulirus*), where both thoracic and abdominal ganglia are fused.

In decapods, nerves to and from the thoracic and abdominal ganglia form connections to legs, swimmerets, uropods and body muscles. In general, the function of the central nervous system is less concentrated in the brain but divided between different ganglia. Some abilities of learning have been demonstrated both in crabs and lobsters.

Sensory receptors

Crustaceans possess a variety of sensory receptors that transmit information to the central nervous system (Brusca & Brusca 2003). Due to the presence of the exoskeleton, chemical and mechanical receptors do not terminate close to the body surface, as receptors of more soft-bodied invertebrates, but terminates below the cuticle. In crustaceans and other arthropods sensory receptors are modified parts of the cuticle itself.

A large number of different chemoreceptor and mechanoreceptors have been described in crustaceans, although their function is usually not known (Bush & Laverack 1982). On the surface, chemoreceptor and mechanoreceptors appears as cuticular processes in the form of hairs, setae and bristles, as well as pores and slits in the cuticle. In most of the receptors, the dendrites of the nerve cell do not penetrate the cuticle itself, but terminate within the underlying epidermis. The dendrites of the nerve cell are affected by the movement of mechanoreceptors or registration of chemical stimuli by the chemoreceptors. In addition to external sensilla, crustaceans are equipped with well-developed proprioceptors. They provide information about the body and appendage position during movement.

The photoreceptors of most crustaceans are compound eyes, which consist of large numbers of units, so-called ommatidia. They are closely packed, and each unit includes a lens, crystalline tract and retina. Nerves from the sensory cells of the retina lead to the brain. In decapods, like crayfish and lobsters, the eyes are situated on stalks, and cover a wide field in all directions.

Apparently, the crustaceans are well equipped with sensory sensilla to keep the animals informed about their surroundings and internal positions. Nerves from the sensory neurons lead to different ganglia in the central nervous system. Compared to the brain at the front of the body, some of the ganglia are relatively large, and the brain is not the only center for reception.

Spiders

Spiders belong to a group of arthropods that is mainly terrestrial, and also includes mites and scorpions. Although some tropical spiders may be kept as household pets, spiders are rarely handled by humans. On the contrary humans often fear them. The central nervous system of spiders has some resemblance to those of crustaceans and insects, but is even more concentrated (Brusca & Brusca 2002). The brain includes a protocerebrum and tritocerebrum connected to ventral nerves, while all the ganglia are more or less fused with the brain. In scorpions the ventral nerve cord has seven ganglia.

Spiders possess a number of sense organs, on which their complex behaviour depends. A large number of the hairs on the surface are mechanoreceptors, and chemoreception involves both airborne smell and taste in liquids. The eyes of spiders are quite different from the compound eyes of insects and crustaceans. Spiders have six or eight eyes, and each eye is supplied with a single lens. The eyes point in different directions and make it possible to look ahead and to the sides at the same time. The two large frontal eyes in hunting species give a sharp picture.

Spiders are extremely efficient predators. They catch their preys in nets or by hunting on the ground. The prey is immobilized by poison, and partly digested externally. Spiders and perhaps scorpions have some ability of learning. Their behaviour may be modified from experience. On the other hand, web-spinning spiders offer some of the most remarkable examples of inherited behaviour among arthropods. The well-known spider webs are constructed according to a strict pattern, although the spider has never witnessed the work of others.

Insects

Diversity

The insects are the most numerous group of all animals. Almost one million species are known, and it is believed that at least a similar number has so far not been discovered. Insects include a variety of forms, like dragonflies, stoneflies, bugs, aphids, fleas, lice, grasshoppers, butterflies, midges and flies [øyenstikkere, steinfluer, tiger, bladlus, lopper, lus, gresshopper, sommerfugler, mygg og fluer]. The beetles [biller] are most numerous, and 350 000 species have been recorded.

Central nervous system

The general tendency for encephalization in higher invertebrates is largely related to the concentration of sense organs at the front of bilaterally symmetrical animals. This is well illustrated in insects. As in other animals the nervous system of insects consists of nerve cells and glia cells (Gillott 1995). Each neuron includes a cell body with extensions; axons. Insect neurons often lack branches of dendrites characteristic of vertebrate nerve cells, although bipolar and multipolar cells do occur. Neurons are aggregated into nerves and ganglia. The nerves include the axon component, while the ganglia are comprised of axons, cell bodies and dendrites. The neurons are surrounded by glia cells with different shapes and functions. Glia cells both serve as isolation and have nutritional functions.

The central nervous system of insects (Figures 4 and 5) consists of series of ganglia joined by paired longitudinal connectives (Gullan & Cranston 2005). In more primitive species there is one pair of ganglia per body segment, but usually the two ganglia of each thoracic and abdominal segment are fused into a single structure. The ganglia of all segments of the head are fused to form two centers; the brain and the suboesophageal ganglion.

The brain is derived from ganglia of three segments, and forms the major association center of the nervous system (Gillott 1995). It includes the protocerebrum, deutocerbrum and tritocerebrum. The protocerebrum is the largest and most complex part of the brain, and contains both neural and neurosecretory elements. Laterally, it is fused with the large optical lobes connected to the compounds eyes. Within the protocerebrum there is a pair of mushroom shaped bodies, so-called because of their outline in

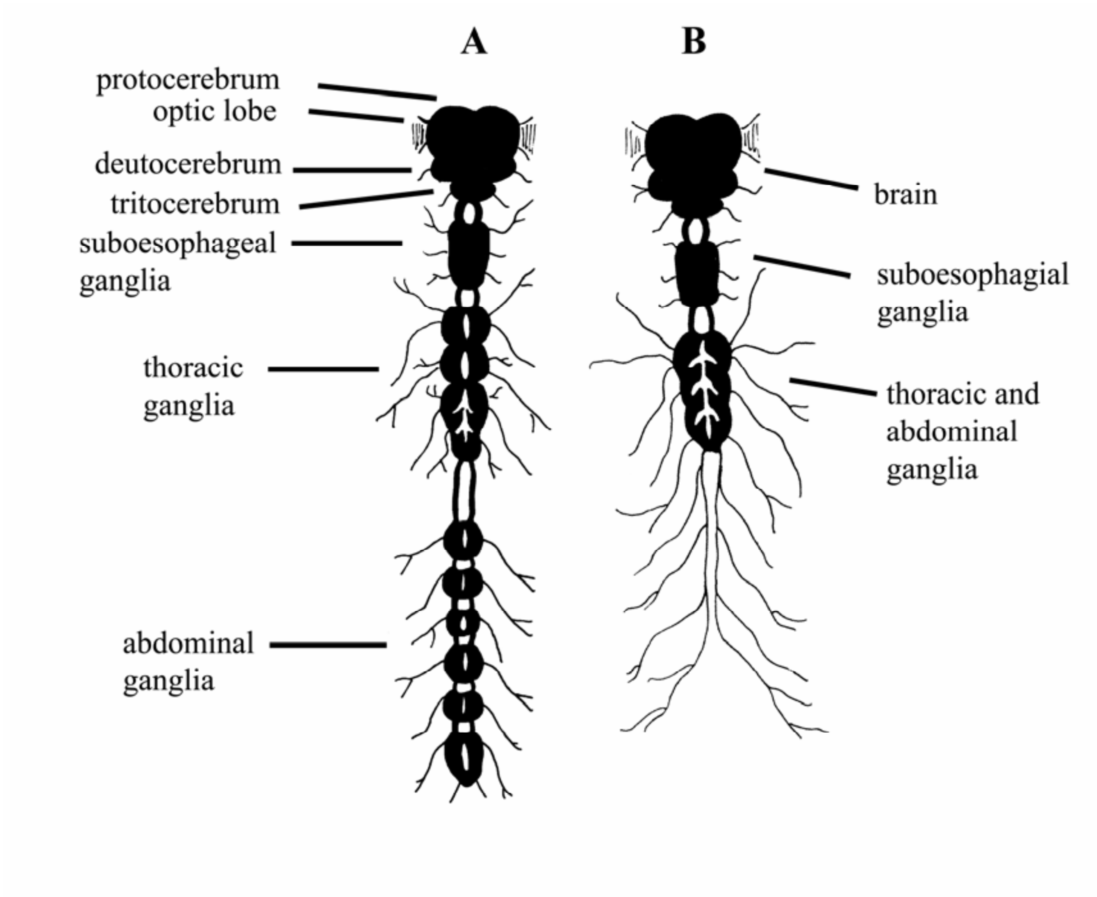

Figure 4. Central nervous system of insects. A. Cockroach (Blattodea), B. Fly (Diptera).

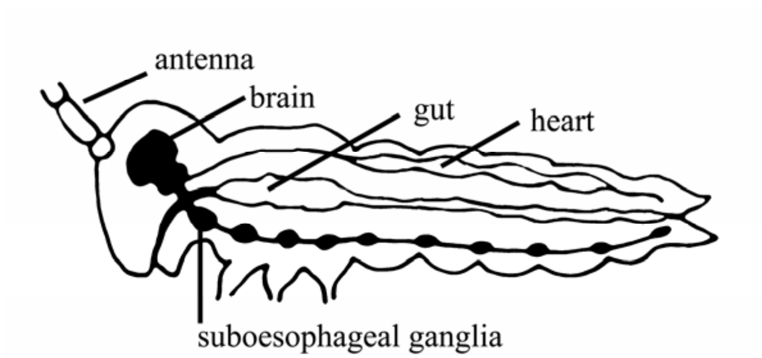

Figure 5. Central nervous system of an insect with brain, suboesophageal ganglia and ventral nerve cord.

histological preparations of the brain. Their size is broadly correlated to the development of complex behaviour pattern, and is most prominent in social insects, like bees and wasps. In worker ants, for example, the mushroom bodies make up one fifth of the brain. The median central body is another part of the brain which appears to coordinate movements and motor activities. The deutocerebrum and tritocerebrum contain neural connection to the senses and muscles of the antennae and upper lips, respectively.
The suboesophageal ganglion innervates other mouthparts and is important for locomotor activities.

In the thorax the thoracic ganglia innervates legs and flight muscles. The abdomen may include up to eight ganglia, but the numbers are often reduced or several ganglia may be fused.

Although there are enormous variations in the morphology of the central nervous system of insects, it represents one of the most complicated systems among invertebrates.

Senses

Insects possess a wide variety of sense organs that are important to monitor and respond to changes in their environment (Gillott 1995, Gullan & Cranston 2005). For example, insects use their senses to find a partner or a source for food, and to register changes in microclimate. To control flight, aerial flows must be sensed and result in appropriate responses.

The insect cuticle is more or less impermeable and represents a problem to the presence of sense organs. They often appear as a weak modifications of the cuticle, and are less numerous than sense organs in many soft-bodied animals. Various types of mechanoreceptors are found all over the body, partly as hair-like structure extending from the cuticle or as more specialized proprioceptors that respond to changes and stresses in the body. Sound reception may be modifications of hair-like receptors or specialized organs with a membrane (tympanum) that responds to air vibrations.

Chemoreceptors are of particular importance for feeding, oviposition and mate location. In social insects the cast system is regulated by chemical clues. A variety of sense organ in insects responds to taste and smell. The detection of sex pheromones in moths over long distances is an example of extremely sensitive chemoreception.

Like crustaceans, insects are equipped with compound eyes. They occupy a large portion of the head surface, and may include several thousand photosensilla or ommatidia. Compound eyes are particularly suited to register moving objects across the ommatidia, like when the scenery changes during flight.

In conclusion, insects are well equipped with sense organs, and probably better than their crustacean relatives in water. Even insect compound eyes are more developed. Active life on land requires swift reactions to the environment. The success on insects as a numerous and highly diversified group of animals is partly due to their effective sense organs.

Learning in insects

It must be pointed out that insects are borne with complex behaviour that cannot be learned. They are genetically programmed to stereotype reaction to different stimuli. In addition, there are numerous examples on how innate behaviour can be modified by learning. Insects may respond to habituation and learn from trial-and-error tests. By associative learning they are able to relate two or more environmental stimuli (Gillott 1995). Memory, which is the ability to store information from the sense organs, has also been widely studied in insects.

Examples of learning in insects include the digger wasp *Philanthus*, which makes an orientation flight in order to remember the vicinity of its nest. Butterflies can learn to find flowers with higher contents of nectar. Grasshoppers learn to avoid harmful plants, and parasitoids learn to locate the habitat of their hosts. Learning has in particular been studied in honeybees (Gould 1993). They can learn to locate food sources by odor and colour. By training they can alter their foraging behaviour, and also learn to recognize shapes and patterns. The memory of honeybees is very persistent. After three visits to a source of sugar, a foraging bee will remember the place forever.

RESPONSES OF INVERTEBRATES TO NOXIOUS CONDITIONS

Nociception

Invertebrates, like vertebrates, have the capacity to detect and respond to noxious or averse stimuli. This capability of animals to detect and react to stimuli that may compromise their integrity is termed nociception (Kavaliers 1988, Smith 1991). The ability to avoid dangers is a fundamental adaptation in all animals, without which they would not be able to survive.

In contrast to the conscious experience of pain, nociception is the unconscious detection of transmissions and responses to noxious stimulations by the nervous system. In other words, nociception indicate the sensory aspects of unpleasant sensations resembling our pain, without presuming our subjective reactions and suffering (Mather 2001).

Averse stimuli include changes in temperature beyond the animal’s normal range, contact with noxious chemicals, mechanical interference or electric shock, all of which would have caused pain in humans. In general, invertebrates respond by withdrawing or escaping to reduce the likelihood of being damaged by the noxious conditions. In most vertebrates, special receptors, or nociceptors, are sensitive to noxious or adverse stimuli, and may be able to code the intensity of the stimulus.

Reflexes

Reflective mechanisms are known from a number of invertebrates. Reflexes allow the animal to escape or withdraw rapidly from dangerous conditions. Series of reflexes may result in more complex behaviour. Graded muscle contractions and coordination of different muscles are based on more complex nervous responses.

Annelids

The segmented annelid worms are sensitive to touch. Mechanical receptors are found all over the body, and nerves from the segmental ganglia innervate the muscles of the body wall (Brusca & Brusca 2002). The reaction of annelids to noxious conditions may be reflexes.

The ventral nerve cord of annelids sometime includes extremely long neurons, or so-called giant fibers, of large diameter. The fibers facilitate rapid conduction of impulses to the brain, bypassing the ganglia of the ventral nerve cord. The fast reaction to touch in earthworms is probably an effect of giant fibers, and result in the rapid withdrawal of the worm. The wriggling of and earthworm on a fishhook is most likely due to reflexes.

Medicinal leaches, *Hirudo medicinalis*, respond by writhing and coiling when their skin is pinched or damaged (Kavaliers 1988). These responses arise from sensory cells, which are in several respects similar to nociceptive cells in mammals, although it is not known if they are equal in function.

Molluscs

Withdrawal reflexes are well known from snails and slugs, and the neural circuit is often relatively short. The withdrawal is graded according to the intensity of the stimulus. Weak stimuli result in local withdrawal, while the whole body is withdrawn following a strong stimulus. Protruding tentacles are at a risk of being snapped by predators, and are quickly withdrawn.

Crustaceans

A dominant feature of many crustaceans is the close connection between neurons and muscles. In this way nerve impulses do not have to pass through the brain, but through ganglia closer to the sensory cells. In crayfish, medial and lateral giant axons cause a fast tail-flip escape response (Krasne & Edwards 2002). If the head of the crayfish is touched, all segments of the abdomen are contracted, and the animal moves swiftly backwards. If the hind end is disturbed, only some of muscles are contracted, and the crayfish makes a somersault away from the disturbances. The reflex arches involved are relatively simple.

Decapod crustaceans exhibit large diversity in behaviour, based on very complex nerve reflexes (Paul et al. 2002). Neural circuits are fractioned into subunits of neurons responsible for different aspects of behaviour and into separate mechanisms to coordinate the activities of these units.

Insects

Reflex mechanisms are well known from insects (Gullan & Cranston 2005). Simple reflex arches may provide for a swift response from a sensory neuron to the subtraction of a muscle. From a sensory hair in the cuticle, an axon leads to one of the ganglia in the central nervous system. In the ganglion the axon connects with one or more interneurons, which are further connected to a motor neuron. From the motor neuron an axon leads to a muscle cell.

Some reflex arches involve so-called giant axons that conduct impulses rapidly from sense organs to muscles through the central nervous system. On example is the extension of the lower jaws in dragonfly nymphs, another is the escape by cockroaches when their cerci are exposes to air movements.

Although the behaviour of insects is complex, it is mainly composed of reflexes (Gullan & Cranston 2005). In some species, however, their behaviour may be modified by environmental conditions and by learning. The stereotype reactions of insects to appropriate stimuli are genetically programmed (Eisemann et al. 1984). In this way their behaviour pattern appear to rely on relatively rigid programmed avoidance and escape responses, triggered by stimuli like heat, chemicals and mechanical touch or restraint.

Cognition

Definitions

Cognition may be defined as higher mental processes in humans and animals, such as the formation of associations, concept formation and insight, whose existence can only be inferred and not directly observed (Henderson's Dictionary of Biological Terms). In ethology, the term is used in a broader sense, including processes involved in acquiring and storing of information from neural impulses (Shettlewood 2001, Braastad 2004). According to Shettlewood (2001), cognition includes perception, learning, memory and decision-making; in short all ways in which animals take in information about the world through the senses, process, retain and decide to act on them. In this way cognitive processes appear at different levels from simple learning to strategically directed behaviour (Braastad 2004). Learning and memory are important parts of cognition and found to different degrees in most animals. At its highest level, cognition, as defined in the dictionary, will lead to sentience and consciousness.

Vertebrates

Duncan (2002) differs between cognition and consciousness as part of higher mental processes in vertebrates. Cognition is used to interpret the external environment and consciousness gives the animal awareness of its internal states. In contrast, simple reflex behaviour in invertebrates at lower levels of the phylogenetic tree is a response to stimuli without awareness. Teleost fish, on the other hand, may demonstrate a level of cognitive development suggestive of sentience (Chandroo et al. 2004).

Cognition in honeybees

Different levels of cognition are found in insects, but most closely studied in honeybees (*Apis mellifera*). The cognitive abilities of bees include the reception of stimuli from the environment and attention to a selective part of the stimuli (Dukas & Real 1993). The information is transferred to the brain for processing, storing and interpretation. Honeybees are able to form cognitive maps, which allow them to locate their position in the landscape. Information stored in the brain of a bee is used to change its behaviour in response to past experience. Honeybees are also able to communicate through behaviour, like in their “dances”, and through odor. In this way they may change the behaviour of other individuals. It appears that honeybees exhibit a relatively high level of cognition, but it is not known if their cognitive abilities also include consciousness.

In addition to bees, it is reasonable to assume that similar levels of cognition may be present in other social insects, and perhaps in more advanced solitary species. With their relatively complicated nervous system and behaviour it cannot be excluded that more advanced insects have some awareness of their existence.

Sentience

Feelings and suffering

Feelings may be described as a specific activity in a sensory system of which an animal is aware (Duncan 2002). The capacity of feeling is termed sentience. In general, it is assumed that most vertebrates, with the exception of fishes, have sentience, but it is not definitely known if it appears in invertebrates. The feeling of pain is an unpleasant sensory and emotional experience associated with damage to tissues or organs. The strong motivation to remove the sources of noxious stimulations is often defined as suffering (Fiorito 1986). The occurrence of suffering in vertebrate animals is connected with physiological and behavioural changes, all of which are known from humans.

Regarding treatment of invertebrates in captivity, the concept of welfare can only be applied to sentient animals (Duncan 2002). In general, there is no concern with lower invertebrates, but consideration should be given to higher invertebrates in which the nervous system is more developed.

For comparative purposes it is interesting to note that there are no neurological bases for assuming that fish might have the capacity for consciousness and pain (Rose 2002). In order to show that fish experiences pain, it is necessary to show that a fish has consciousness. This depends on a specific area of the brain, namely the neocortex regions of the cerebral hemisphere, which are absent in fishes. According to Chandroo et al. (2004), recent work regarding consciousness in fishes yields no consensus. Still, teleost fish demonstrate functional similarities at a level of cognitive development suggestive of sentience.

Pain

Invertebrates react in different ways to detrimental stimuli (Fiorito 1986). The reactions do not necessarily in itself indicate any experience of pain, but more an activation of the central nervous system to produce avoidance or escape reactions. For example, due to mechanical stress, the spider *Argiope* sp. may react with leg autotony, and the crab *Carcinus mediterraneus* with alarm display.

Pain in Cephalopods

As pointed out earlier, cephalopods have a centralized nervous system, which is often described as a brain (Smith 1991, Mather 2001, Nixon & Young 2003). It has even been suggested that the cephalopod brain is analogous to the cerebral cortex of higher vertebrates.

The great ability to learn in squids and octopuses, described above, suggests that they are also able to experience pain. Still, the evidence for pain reception is uncertain. Cephalopods, however, exhibit body postures, colour patterns and behaviour that resemble those of pain, or at least show that something is wrong.

As an example, cited from Mather (2001), “Octopuses stung by a sea anemone protectively placed on the shell of a hermit crab do not just retreat. They may circle around as if planning to attack the crab and anemone from the rear. They may climb up the side of the aquarium and reach an arm or two around the sea anemone. One of the ones I tested sneaked - tiptoeing on arm suckers - along the aquarium bottom, getting close enough to grab the hermit crab without having to leap and encounter the anemone. Several enterprising octopuses aimed strong jets of water at the anemone, as if hoping to blow it off the shell.”

While Duncan (2002) thinks that cephalopods are almost certainly sentient, Mather (2001) points out we really do not know how to tell if octopuses have emotions. When faced with dilemmas, octopuses may change to a pale colour associated with fright, or to a red colour seen as anger. Evidence of aversion, emotion-like responses and cognitive ability to treat a difficult situation, as in the example with the sea anemone, all resembles very much the responses of higher vertebrates to threat and pain.

Pain in insects

On the question of pain in insects, Eisener et al. (1984) pointed out that it is not possible to give a conclusive answer since the subjective experienced of an organisms cannot be registered. Still, from considerations of the insect nervous systems and their behaviour there does not appear to be any support to the occurrence of pain. Several examples are known in which insects continue with normal activities even after severe injury (Eisener et al. 1984, Smith 1991). An insect walking with a crushed foot will apply it to the substrate with undiminished force. Locusts [vandregresshopper] have been seen to continue feeding whilst being eaten themselves by preying mantis [kneler], and aphids continue to feed when eaten by coccinelid beetles [marihøner]. A male mantis continues to mate although eaten by his partner, and a tsetse fly will try to suck blood although half dissected during an experiment. Many adult insects and larvae continue to develop whilst being eaten by large internal parasitoids. It appears that there is no evidence of conscious experience in insects, since natural selection of a capacity for pain would also result in corresponding capacity for adaptive responses.

Furthermore, it is argued that although some insect behaviour, such as the convulsions of insects poisoned by DDT, the struggling of restrained insects, repellent secretion and alarm pheromones, resembles that of higher animals responding to pain, no more requires the presence of pain sense than reflexive withdrawal.

In spite of these strong arguments against pain in insects, more research is wanted. Some authors think that it is presumptuous for us to assume that because our human suffering involves self-awareness, this should also be true in other species. Wigglesworth (1980) recommended that insects for experimental purposes have their nervous system inactivated prior to traumatizing manipulation.

Pain in Decapods

The nervous system of lobsters has been extensively studied because it serves as a model of simple neural circuitry. Still, it is not clear if the lobster can feel pain. Lobsters react violently when dropped into boiling water. Many people believe that this is an expression of pain, but it is reasonable to consider their reactions as reflexes to noxious stimuli. Several methods are suggested to reduce any possible stress in crabs and lobster before boiling. They include slow heating, transfer to saturated NaCl or fresh water, as well as cooling.

Are we mistaken?

As pointed out by Sherwin (2001), we may be mistaken in assuming that invertebrates have a reduced capacity to experience suffering. Suffering is a private experience, or a negative mental state that cannot be measured directly. The responses of invertebrates to noxious conditions are often strikingly similar to those of vertebrates. Several experimental studies have shown that invertebrates such as cockroaches, flies and slugs have short and long-term memory, have ability of spatial and social learning, perform appropriately on preference tests, and may exhibit behavioural and physiological responses indicative of pain. The similarity of these responses to those of vertebrates may indicate a level of consciousness or suffering that is normally not attributed to invertebrates.

Opioids

Opioids are substances that mimic the effects of opium in the brain, e.g. peptides like enkephalins and endorphins. Naloxene is a compound that blocks the effects of these substances. In mammals and other vertebrates, opioid peptides that are produced in the body can modify nervous transmission of nociception. The result is an analgesic effect or relief from pain (Fiorito 1986, Kavaliers 1988, Smith 1991). Injections of substances that mimic the effects of the endogenous opioids, like morphine, also produce analgesis and may reduce behavioural responses to noxious stimuli. Furthermore, naloxene may suppress the analgesic effects.

Opioid substances are also known from invertebrates. If their function is similar to that in vertebrates, this is an indication that invertebrates may feel pain, which is reduced by the opioids. At present no certain conclusion can be drawn, but opioids are interesting in considering the question of pain in invertebrates. Examples of the presence of opioids are known from different groups of invertebrates.

Under experimental conditions, low doses of opioid peptides and morphine affects behaviour in the garden snail *Cepaea nemoralis*. The substances increase the time taken for a snail to respond by lifting its foot when placed on a hot plate at 40 ºC. Furthermore, naloxene abolishes the effect of morphine. Morphine and naloxene also affect the defensive responses of the mantis shrimp (*Squilla mantis*) to electrical shock. Similar effects are known from insects like the honeybee and the praying mantis *Stagmatophora biocellata*. Opioid substances are also found in animals with relatively simple nerve systems. They probably play a role in sensory modulations of the earthworm *Lumbricus terrestris*, and injections of naloxene inhibit the wriggling and escape responses of the worms.

According to Kavaliers (1988), the presence of opioids in a variety of invertebrates suggests that modulation of adverse and nociceptive responses was present at an early stage of the evolutionary history. It is unlikely that similar neuromodulary mechanisms have arisen independently in various phyla of animals. The question remains why they should be present in invertebrates if these animals do not feel any pain.

CONCLUSIONS

Central nervous system

The central nervous systems of invertebrates show different levels of complexity. Echinoderms [Norwegian: pigghuder] have a simple net of nerves, but no distinct ganglia. In annelids [leddormer] and arthropods [leddyr] the nervous system comprises an anterior brain and a ventral nerve string with ganglia corresponding to the segmentation of the animal (Figure 5). Molluscs [bløtdyr], bivalves [muslinger], snails and slugs are equipped with simple pairs of ganglia in different parts of the body (Figure 1). In cephalopods [blekkspruter], and in particular in the eight-armed octopuses, the ganglia are concentrated in a large and complex brain (Figure 2).

The phylogenetic tree of the animal kingdom was divided in two branches several hundred million years ago. Vertebrates and echinoderms belong to one of the branches, and most invertebrates to the other one. With their long evolutionary history, the nervous system in vertebrates and invertebrates are quite different. In contrast to invertebrates, the vertebrates have compact brains and a dorsal nerve cord. Certain areas of the vertebrate brain are sites of consciousness. The great differences make it difficult to compare the cognitive abilities of vertebrates and invertebrates. Since they lack the cerebral cortex responsible for pain in mammals, it is uncertain if fish can feel any pain. Invertebrates also lack these structures, but it cannot be excluded that parts of their nervous system have similar functions.

Senses

Through their neural systems, all animals react to noxious or dangerous stimuli that could result in damage to their skin or other organs. The escape mechanisms in animals are essential adaptations partly based on reflexes, and not necessarily associated with conscious experience. Most invertebrates are equipped with numerous mechanical and chemical sense organs. Compound eyes are well developed in decapod crustaceans [tifotkreps] and insects, and cephalopods have eyes resembling those of vertebrates. In contrast to vertebrates, most sensory neurons in invertebrates are monopolar. The sense organs respond to stimuli from the environment, and axons from sensory neurons lead to different ganglia in the central nervous system.

Nociception and reflexes

The capacity of animals to react to harmful stimuli is called nociception. In contrast to pain, nociception is the unconscious response to noxious stimuli. Rapid withdrawal in invertebrates is often based on short neural circuits from neural cells to muscles. Some rapid reflex arches include so-called giant nerve fibers. Examples of reflexes are the reaction to air movements in cockroaches [kakerlakker], flapping of the tail in lobsters [hummer] and hiding of the antennae in snails. The occurrence of series of reflexes is known from insects.

Most of the behaviour in invertebrates, even very complex ones, is inherited. In this way, behavioural patterns rely on rigid programmed avoidance and escape responses. To different degrees, behaviour is also modified by learning, in particular in octopuses and social insects.

Cognition

Cognition includes processes involved in acquiring and storing information from neural impulses. Learning and the control of strategically directed behaviour are parts of cognition. Cognitive abilities of insects are best known from honeybees [honningbier], and octopuses apparently possess a high level of cognition.

Sentience and pain

The capacity of feeling is called sentience, and is the basis for experience of stress and pain. It is assumed that four-legged vertebrates are sentient, but it is not definitely known if this is the case in fishes. In invertebrates, more research is required to show if they have sentience or consciousness. The function of opioids in invertebrates is not known, but the production of such substances reduces pain in vertebrates.

With the relatively simple nervous system of earthworms [meitemark] and other annelids, it is very unlikely that they can feel any pain. The wriggling of earthworms on a hook can be considered as reflexes.

In molluscs like snails, slugs and clams, the nervous system includes several ganglia, but their brains are poorly developed. Sentience in these animals is unlikely. In contrast, the brains of cephalopods, and in particular of octopuses, include large concentrations of ganglia. Although octopuses have a high level of cognition and great ability to learn, it is not definitely known if they can experience pain. Among invertebrates, however, cephalopods are definitely the animals that should be given the highest consideration when handled and kept in captivity. In Norway this also applies to *Todarodes saggitatus* [akkar], which is seafood for humans, even if this species does not belong to the highest developed cephalopods.

In spite of the violent reactions of lobsters and crabs when put in boiling water, it is assumed that these are reflexes to noxious stimuli. Different kinds of pretreatment before boiling may reduce any possible feeling of stress. There is apparently a paucity of exact knowledge on sentience in crustaceans, and more research is needed. Lobsters and crabs have some capacity of learning, but it is unlikely that they can feel pain.

The nervous system and senses of insects appear to be better developed than in crustaceans since an active life on land may be more demanding. With the great diversity of insects, there are great differences in the organization of the central nervous system and senses. In general, insects are equipped with numerous sense organs. The brain is particularly well developed in social insects, and the size of certain neural centers can be correlated with learning capacity. Learning is also known from many solitary species of insects. Insects do not react to damage of their bodies, but may show strong reflexes to constraint. With our present knowledge, it is usually concluded that insects cannot feel pain. Still, doubts have been raised. Among invertebrates, social insects represent a high level of cognition, and their welfare should be considered during handling.

Concerns

In conclusion, it appears that most invertebrates probably are unable to feel pain. As long as the questions of sentience and pain remain uncertain, however, concern should at least be given to more advanced species of invertebrates during handling and in captivity. Cephalopods and social insects may be particularly vulnerable. A definite answer to pain in invertebrates may be difficult to find. In the meantime, efforts should be made to maintain these animals in the most appropriate way during handling and confinement, giving them the benefit of doubt in situations that have a potential to cause pain and stress.

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