

MANIPULATIVE MOTOR ACTIVITY OF THE CUTTLEFISH SEPIA OFFICINALIS
DURING PREY-CAPTURE

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ABSTRACT

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Following capture by the cuttlefish Sepia officinalis, crabs are manipulated by active movements of all eight arms to facilitate prey paralysis and ingestion. This manipulative behaviour is described for the first time. Prior to ingestion the prey is regularly held in a specific orientation, termed the "reference position", irrespective of the initial angle of attack. Prey capture is followed by an initial, very rapid manipulative phase, bringing the cephalo-thorax-abdomen junction of the crab to lie adjacent to the mouth of the cuttlefish. In this position the cuttlefish can inflict a wound, usually to the proximal joints of the hind pereopod. The salivary toxins are probably injected into this wound provoking a rapid paralysis of the prey. A second manipulative phase orientates the crab into the "reference position". This phase involves complex coordinated movements of the arms that can, in some cases, rotate the crab by up to 180°. Suppression of visual input has little effect on this behaviour. Tactile input concerning the position and movements of the pereopods would appear to play an important rôle in the execution of this manipulation. Sensorial control of this behaviour and the possible existence of muscular receptors capable of detecting movements are discussed.

KEY WORDS

cephalopod - Sepia - prey-capture - manipulative motor activity

INTRODUCTION

The predatory behaviour of the common cuttlefish Sepia officinalis has been the subject of numerous descriptive and experimental studies (Wilson, 1946 ; Boycott, 1958 ; Boulet, 1964 ; Messenger, 1968, 1977 ; Duval et al., 1984 ; Nixon, 1985 ; Chichery and Chichery, 1987). This behaviour can be split into three phases :

attention, positioning and attack (Messenger, 1968).

The first two phases are visually guided motor activities, whereas the attack is under open-loop control (Messenger, 1968 ; Chichery and Chichery, 1984). The prey is attacked by one of two strategies : either by ejection of the two tentacles or by jumping on the prey. The size of the prey (crab) relative to that of the predator has been shown to be important in the choice of attack strategy (Duval et al., 1984). Small crabs are preferentially captured by tentacle ejection and large crabs by jumping. It is evident that the capture of large crabs entails some risk to the predator. The cuttlefish has therefore developed various means to avoid injury caused by the defensive activities of the prey.

Many authors (Boycott, 1958 ; Boulet, 1958 ; Messenger, 1968) have observed the cuttlefish to position itself behind the crab facilitating a postero-dorsal attack. This behaviour, though frequent, is not exclusive : frontal and lateral attacks have also been noted by the above authors. This flexibility of attack implies a capacity for precise manipulation in order to avoid injury from the crab's claws. Thus, the predatory behaviour of the cuttlefish can be divided into two groups of motor activity. The first group is constituted by the postural-kinetic movements comprising the three phases described by Messenger (1968) while the second group is characterized by manipulative movements leading to prey ingestion (fig. 1 ; see also Chichery and Chichery, 1987). This evident manipulative activity of the cuttlefish has never been studied in detail.

In the present paper this behaviour is described for the first time. This description forms the behavioural reference for on-going neuroethological studies of the predatory behaviour of this species (Chichery and Chichery, 1987).

MATERIAL AND METHODS

Adult Sepia officinalis (dorsal mantle length ≥ 140 mm) were caught in the vicinity of Luc-sur-Mer. They were maintained in running, filtered sea water. In order to facilitate the observation of the manipulatory behaviour only large crabs (Carcinus maenas ; carapace width across the widest points ≥ 50 mm) were used as prey. As posterior attacks lead to minimal manipulative movement, crabs were always presented head-on. This increases the probability of lateral and frontal attacks, though the experimental aquarium was

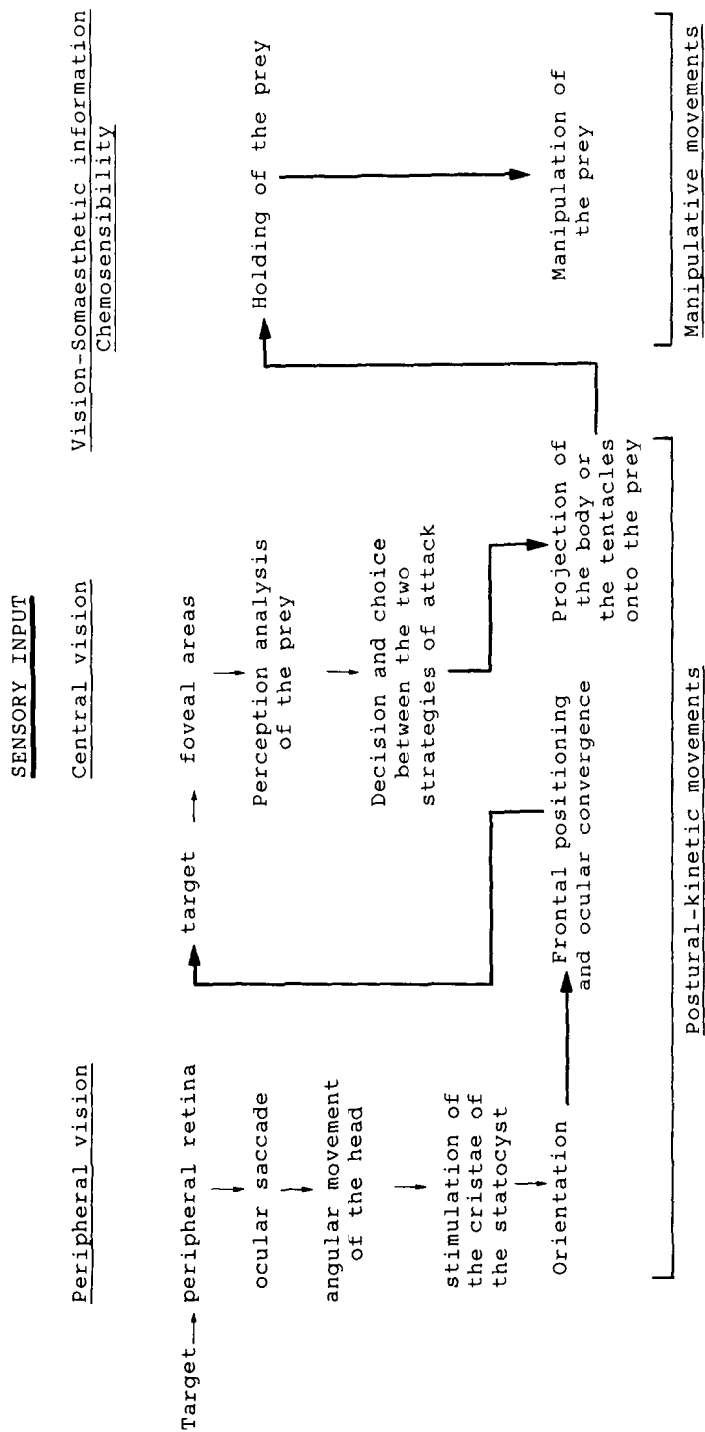


Fig. 1. Functional diagram of the different stages of the predatory behaviour.

sufficiently large to allow the cuttlefish to reposition itself.

A second series of experiments was designed to study the relative importance of sensorial inputs (vision, somaesthetic information, chemosensibility) in the control of manipulative behaviour. These experiments were carried out in a dark room. The visually guided first stages of the predatory behaviour were observed under subdued lighting, the angle of attack was noted and the room obscured at the moment of prey seizure. After 3 minutes the subdued lighting was turned on again and the position of the cuttlefish's arms noted.

RESULTS

Variations of attack angle and pre-ingestive "reference position" of the prey.

The variability of attack angle has been confirmed (table I). It has been observed that, prior to ingestion, the crab is nearly always held in a specific position (hereafter termed "reference position" ; table I). In this "reference position", the most dorsal arms (pairs 1 and 2 ; Robson, 1929) are applied to the dorsal face of the carapace, the third pair encircle the crab laterally and the ventral arms (4) hold the crab ventrally. In only five (out of 126) attacks was the "reference position" not observed.

TABLE I

Incidence of post-seizure prey rejection, manipulative behaviour and adoption of the "reference position" in control animals.
N = Number of attacks observed.

| | Posterior attacks | Lateral attacks | Frontal attacks |
|---------------------------|----------------------|--------------------|--------------------|
| N | 31 | 52 | 43 |
| Rejection | 0 (0%) | 1 (1.9%) | 7 (16.2%) |
| Manipulative behaviour | 31 | 51 | 36 |
| "Reference position" | 31 (100%) | 50 (98%) | 32 (88.8%) |

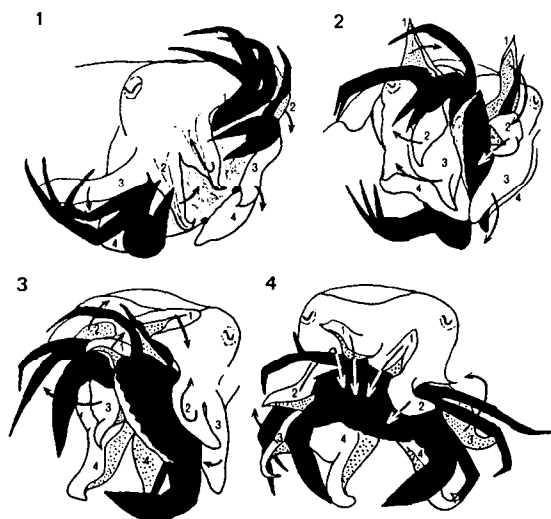


Fig. 2. Annotated diagram of the second manipulative phase redrawn from consecutive photographs taken at two second intervals. The cuttlefish's arms are numbered 1-4, their respective movements are indicated by arrows.

TABLE II

Time lapses (sec \pm 1SD) between various phases of the attack.

| | All attacks | Posterior attacks | Lateral attacks | Frontal attacks |
|--|-----------------|-------------------|------------------|-----------------|
| Seizure to pereiopod trembling | 54.9 \pm 13.1 | 56.2 \pm 14.1 | 52.7 \pm 11.1 | 56.2 \pm 14.6 |
| Seizure to the beginning of the 2nd manipulative phase | | | 86.8 \pm 26.6 | |
| Seizure to the end of the 2nd manipulative phase | | | 133.9 \pm 46.5 | |

Two crabs, one attacked laterally and the other frontally, were positioned vertically with respect to the cuttlefish, the cephalothorax-abdomen junction orientated towards the mouth. A further two frontally attacked crabs were held in similar fashion to the "reference position" but with the anterior of the crab orientated towards the mouth. Finally one frontally attacked crab was positioned upside-down with respect to the "reference position".

Description of manipulative sequences.

Posterior attacks.

Crab seizure by the arms or by the tentacles is followed by an initial manipulative phase lifting the crab such that it cannot gain a purchase on the substrate. During this phase, which lasts for one to two seconds, the extremities of the cuttlefish's arms are turned back in order to avoid the crab's claws. The cephalothorax-abdomen junction is thus brought to lie in front of the predator's mouth. The first stages of paralysis, induced by the absorption of salivary toxins, is generally observed as a convulsive trembling of the pereopods. Following paralysis, the crab is reorientated, if necessary, into the "reference position".

Lateral and frontal attacks.

Lateral and frontal attacks are virtually always followed by a very rapid (≤ 2 sec) manipulation of the prey. As with the posterior attacks the cephalothorax-abdomen junction is orientated towards the mouth. Whereas in the former case the carapace is held horizontally, following lateral or frontal attack the orientation of the crab is variable. Once again the extremities of the cuttlefish's arms are turned back and pereopod trembling is the first sign of paralysis.

In these more difficult attacks, the second manipulative phase is more evident and remarkable for the precision of its execution. The cuttlefish progressively rotates the crab by the sequential utilisation of all eight arms (fig. 2). In most cases (table I) the crab is brought to lie in, or close to, the "reference position".

Variability of temporal organization.

Based upon the time lapse between prey seizure and pereopod trembling two groups of attacks can be distinguished. In the first most frequent (111/118), group of attacks the first manipulative phase was always observed, regardless of the angle of attack (table II). In the second, infrequent (7/118) group, prey seizure

was not followed by the first manipulative phase. In these seven exceptional cases the time lapse prior to pereopod trembling was abnormally long and very variable (270 s, 135 s, 150 s, 240 s, 160 s, 480 s, 240 s).

Modalities of poisoning.

The literature suggests that prey-paralysis is achieved by the diffusion of salivary toxins in the branchial cavities of the crab (Ghiretti, 1960 ; Messenger, 1968). In these experiments, however, it was noted that prey-paralysis was always accompanied by a small wound to the crab, in the majority of cases at the base of the last pair of legs (table III).

TABLE III

Distribution of wounds inflicted by the cuttlefish on the exoskeleton of seized crabs (*Carcinus maenas*). The crabs were recovered for examination within twenty seconds after seizure. In some cases the wound affects two adjacent joints.

| | N | Coxopodite | Articular membrane coxopodite- basipodite | Basi- ischio- podite | Meropodite | Number of crabs paralysed |
|-------------|----|------------|--|----------------------------|------------|---------------------------------|
| Pereiopod 5 | 40 | 12 | 23 | 9 | 3 | 40 |
| Abdomen | 4 | | | | | 4 |
| No wound | 12 | | | | | 0 |

Relative importance of sensorial inputs.

When visual input is interrupted by obscuring the aquarium, prey manipulation is little affected (table IV). The incidence of post-seizure prey rejection is slightly higher in darkness (cf. tables I and IV). This difference, however is not significant (χ^2). Unilateral or bilateral pereopod removal influences the post-seizure orientation of the crabs by the cuttlefish (table V). The occurrence of the "reference position" is greatly reduced.

TABLE IV

Manipulative behaviour in darkness. Incidence of post-seizure prey rejection and adoption of the "reference position" observed at the end of 3 minutes in total darkness and the incidence of remanipulative movements following these 3 minutes of darkness.

| | Posterior attacks | Lateral attacks | Frontal attacks |
|----------------------|-------------------|-----------------|-----------------|
| No. of attacks | 13 | 21 | 14 |
| Prey-rejection | 0 (0%) | 1 (4.7%) | 5 (35.7%) |
| "Reference position" | 13 (100%) | 17 (85%) | 8 (88.8%) |
| Remanipulation | 0 | 3 | 1 |

TABLE V

Influence of pereopod removal.

| Pereopod removal | N | Prey-ingestive position of the crab with respect to the cuttlefish's mouth | | | |
|-----------------------|----|--|---------------------------------------|----------------------|---------------------|
| | | No. of reference position | No. of reference position upside-down | No. of lateral right | No. of lateral left |
| Bilateral | 16 | 7 | 3 | 4 | 2 |
| Unilateral left-side | 9 | 4 | 0 | 0 | 5 |
| Unilateral right-side | 11 | 6 | 0 | 5 | 0 |

DISCUSSION

Tactile performance and manipulation by cephalopods.

The tactile performance of cephalopods, especially Octopus, has been well described from discriminative learning experiments (see reviews by Wells, 1978 ; Young, 1983). The manipulative capacities of these animals during natural behaviour, however, have been little studied. Octopus can use its arms to wrest a crab from various containers (Piéron, 1911 ; Cousteau and Diolé, 1973). Boyle and knobloch (1981) have shown that Eledone cirrhosa positions the

borehole that it makes in the carapace of various crabs with relative consistency. This implies a manipulation of the prey prior to boring. Owing to the arm length of Eledone this manipulation is more difficult to observe than in Sepia.

First manipulative phase and prey paralysis.

It is evident from these results that the first manipulative phase serves to orientate, as quickly as possible, the crab with its cephalothorax-abdomen junction towards the mouth of the cuttlefish. In this position the cuttlefish is able to inflict a small wound, probably aimed at the vulnerable coxopodite-basipodite articular membrane, facilitating the penetration of salivary toxins. In the rare cases in which this manipulative phase was not observed, prey paralysis was apparently hampered, the time lapse prior to pereopod trembling being significantly increased. The rapidity of execution of this phase leads to a homogeneity in the trembling time lapse regardless of the angle of attack (table II).

Second manipulative phase and "reference position".

The "reference position" is an important feature of predation by the cuttlefish, being observed in virtually every case. The execution of this phase implies a very fine motor control of the arms and suckers.

It is noteworthy that this phase begins about 30 s. after the start of pereopod trembling (i.e. when the crab is, or is nearly, paralysed). It would, thus, seem that the cuttlefish perceives the paralysis of its prey and can therefore minimise the risks of injury by the crab.

Sensorial control of manipulation.

The occurrence of precise manipulative activity in cephalopods is of little surprise on account of the flexibility of their arms. Such behaviour implies fine sensory-motor coordination involving various sensorial inputs (visual, tactile, proprioceptive, chemoreceptive). Cephalopod visual capacity has been extensively studied (see reviews by Wells, 1978 ; Messenger, 1981).

Tactile abilities have also been well described (see reviews by wells, 1978 ; Young, 1983), the numerous suckers facilitating the exploration of the environment. The anatomy of these suckers has been studied in some detail by Graziadei (1964a,b ; 1965a,b) who has described the different groups of muscles and their sensory and motor innervation. There would appear to exist at least four morphologically distinct types of receptors, certain perhaps corresponding

to mechanoreceptors, others perhaps being chemoreceptors. Nixon and Dilly (1977) have observed tufts of cilia protruding from pores on the outside of the cuttlefish's suckers. The position of these pores suggests that the tufts of cilia correspond to the ciliated endings of chemoreceptors described by Graziadei (1964b). Octopuses also possess muscular stretch receptors in their arms (Graziadei, 1965b). Touch learning experiments (Wells and Wells, 1956 ; Wells, 1961 ; Wells, 1964a,b) have contributed a great deal to our knowledge of the tactile capacities of Octopus. Though Octopus can distinguish, by touch, objects which differ in their proportion of surface irregularities, they fail to distinguish between objects that differ in the arrangement or orientation of their surface irregularities. Likewise they fail to distinguish between objects of different form or weight. These results indicate that cephalopods do not possess receptors capable of recording arm and sucker position independently of muscle tension and are thus unable of discerning the position of their arms other than by observation (Wells, 1978). The electrophysiological work of Rowell (1966) confirms these behavioural data, none of the neurons recorded in the arm cord showed an electrical activity correlated with positional information.

The importance of tactile, and perhaps chemosensorial, input has been demonstrated in the present experiments. Crab manipulation in complete darkness illustrates the secondary rôle played by visual input in contrast to its primary rôle in the other phases of predatory behaviour (Messenger, 1968 ; Chichery and Chichery, 1984).

Positional information could be provided by the chemical stimulus of the cephalothorax-abdomen junction detected by the chemoreceptors of the lips (Graziadei, 1965a). It would appear that tactile perception of pereopod position (table V) plays an important rôle in the orientating of the crab into the "reference position".

During the first manipulative phase the crab is orientated by the proximal suckers, the arm tips being folded back to avoid injury. Around the mouth the position of the arms is relatively fixed and in this position the animal does not require proprioceptive input to form an internal map of the relative positions of the arm and sucker receptors. Thus, in this phase, crab manoeuvres could be achieved on the basis of sensory input from contact re-

ceptors alone. During the second manipulative phase, however, arm movements are more extensive involve the whole arms, in this case, therefore, it would appear inappropriate to exclude the use of proprioceptive information.

The structural variability of proprioceptors, and the difficulties encountered in experimentation, has often led to controversy over their existence (for example the proprioceptors of the extrinsic muscles of the vertebrate eye). Recently, Kier et al. (1985) have provided some evidence for the existence of mechanoreceptors in the fins of the cuttlefish. The presence of afferent fibres, originating from the arm and/or sucker musculature, in various lobes of the supraoesophageal mass (Budelmann and Young, 1985, 1987) and in the peduncle lobe (Camm et al., 1985) has been demonstrated by neurohistological techniques. These lobes are known to be involved with fine motor control. It is evident, therefore, that more detailed studies of the existence of muscle positional receptors are desirable.

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