

## THE VISUAL ATTACK OF THE CUTTLEFISH, *SEPIA OFFICINALIS*

By J. B. MESSENGER

Anatomy Department, University College, London and Stazione Zoologica, Napoli\*

This paper presents evidence that the attack of the cuttlefish, *Sepia officinalis*, is visually initiated and controlled and that interference with the visual system lowers its accuracy. It also presents the first evidence that cuttlefish make visually-induced (*fixation*) eye movements and that these occur in a direction compatible with the assumption that there is an area of special sensitivity in the retina.

The cuttlefish is an active predator, like all known coleoid cephalopods; it feeds on small crustaceans, on fish, or even on smaller *Sepia*. The prey is generally captured by means of suckers on the ends of two extensible tentacles, which are rapidly shot out towards the prey and then retract to bring the prey to the arms and mouth.

The attack of *Sepia* on prawns was first described by Sanders & Young (1940) who showed that the attack was not modified if certain parts of the supra-oesophageal brain were removed, but that the ability to follow the prey when it leaves the visual field was impaired by these operations. Their implicit recognition that the attack in *Sepia* is visual did not prompt investigation, however, and neither Holmes (1940) nor Wilson (1946), whose excellent photographs are well-known, drew attention to the visual nature of the attack. Wilson, for example, merely says that '*Sepia* . . . turns to face its prey'. Wells (1958) has a good description of the attack of newly hatched cuttlefish and notes the occurrence of eye movements but Boulet (1958), who analyses the visual stimuli that elicit attack, does not describe the attack though he also records eye movements.

The eyes themselves, which are very large, have been described by many workers, notably Alexandrowicz (1927); and the existence of a complete set of extrinsic eye muscles has been known since the work of Glockauer (1915). The retina has been recently studied by Young (1963a).

### Methods

Subjects were young and adult *Sepia officinalis* L., mostly males (Wells, 1962), taken in the Bay

of Naples, transferred to the laboratory in wooden buckets and kept singly in opaque plastic or in glass tanks. The floors of the tanks were not covered with sand but *Sepia* survived well in them for over 2 weeks. The adults ranged in size from about 40 to 120 mm dorsal mantle length, but generally they were about 90 to 100 mm long. Very young *Sepia*, hatched from eggs in the laboratory, were also studied. These were about 2 weeks old and had dorsal mantle lengths of 6 to 7 mm. Subjects were fed on prawns (*Leander*, sp.), small crabs (*Carcinus maenas*), or young fish (*Mugil*, sp.).

The animals were observed in the aquarium and photographed under floodlight (Kodachrome IIA film) or daylight (Ilford Mark V film) using a 16-mm ciné-camera. Subsequently the films were analysed frame by frame.

The accuracy of the attack of normal *Sepia* was also recorded and the effect of interference with certain parameters in the attack situation was tested.

Animals brought in from the sea were left for 2 days in their tanks. On the third day a 'lure' prawn was introduced into the tank. This was alive but had black thread tied round the abdomen just anterior to the telson. It was dropped into the tank (and if necessary pulled by the thread) so that it fell into the visual field of one eye. The *Sepia* was watched for reaction: a hungry *Sepia* responds within the first 5 sec by colour changes, eye and body movements. When this occurred the lure was removed and a free live prawn substituted for it. The cuttlefish was allowed to attack and the number of errors made (i.e. missed shots) was recorded. If after 2 min the cuttlefish had not attacked, the prawn was removed by net. If the cuttlefish did not respond to the lure in 30 sec, the latter was removed and no free prawn was given.

The attack was studied in two groups of animals. Group I, in the spring of 1966, were kept in white tanks and group II, in the autumn of 1966, occupied dark grey tanks. Both grey and white tanks had similar dimensions: 100 cm × 30 cm, with water 40 cm deep, and over one end of the tank was a white strip-light (40 W). The position of the cuttlefish at the start of the trial was not constant. In the spring the water

\*Present address: Department of Zoology, The University, Sheffield 10

temperature ranged from 16 to 19°C; in the autumn it ranged from 14 to 19°C.

### Surgical Procedures

To analyse further the visual attack system the sensory side (eyes) and motor side (arms and tentacles) of the system were surgically interfered with.

The operations were performed under anaesthesia, using a 1 per cent solution of urethane in sea water. At such a concentration urethane induced anaesthesia in about a minute. Recovery, which took only slightly longer, was facilitated by passing a jet of water over the gills. During the operations, which in no case lasted more than 2 min, it was found to be unnecessary to maintain oxygenation of the gills.

Three kinds of operations were made:

(1) *Tentacle removal (unilateral and bilateral)*. The tentacle was withdrawn from its sac by toothed forceps, stretched to its full length and cut off close to its base with scissors.

(2) *Arm removal*. The arms were cut off with scissors, close to their point of separation from each other. The stump remaining was less than a quarter of the total arm length.

(3) *Blinding (unilateral and bilateral)*. *Sepia* bleeds to death if the orbit is opened, so that it is impracticable to blind the animals by optic nerve section. Another 'blinding' technique was therefore devised; the iris is cut away, the lens is removed, the posterior chamber fluid is expelled, and the two edges of the skin around the eyes are sutured. Although such an operation leaves the retinal elements intact no behavioural responses are observed in binocularly 'blinded' preparations, even after gross changes in light intensity. Nor do the preparations respond to approaching large objects, which elicit escape movements in intact *Sepia*. After monocular 'blinding' the animal only responds to visual stimuli in the visual field of the intact eye. We are confident, therefore, that this operation renders the animal functionally blind in the operated eye. Throughout the text the term 'blind' describes a preparation that has undergone such an operation.

Although it is now established that there may be other light receptors sited deep within the body of cephalopods (Nishioka, Yasumasu & Bern, 1966; Messenger, 1967a), these organs are thought to be concerned with long-term metabolic regulation. The organs were not removed in the present study but it is maintained that their persistence does not invalidate the conclusions drawn from it.

### Definitions

The cuttlefish has the typically decapod arrangement of eight short *arms*, used for various activities, and two long *tentacles*, used to seize the prey. The arms are numbered 1 to 4 (Robson, 1929) so that the most dorsal and central pair are referred to as the first pair, while the lateral and ventral wedge-shaped arms are the fourth pair. The terms 'dorsal' and 'ventral' are not morphological; they refer to the orientation adopted by the animal in life (Hoyle, 1886). As an estimate of size, dorsal mantle length is used (Robson, 1929) although the weight would be a much more sensitive measure (Nixon, 1966). A general account of the anatomy of *Sepia* is given in Tompsett (1939); the brain is described in detail by Boycott (1961), who also gives the best short account of the biology of *Sepia* (1958).

The term *yaw* is used conventionally, so that the yawing plane is horizontal. This is shown in Fig. 1, which also defines the *body axis* and the *optical axis*. The eye whose visual field the prawn first enters is termed the *stimulated eye*; the contralateral eye is then the *unstimulated eye*.

**The eyes.** In cuttlefish these are so situated that their visual field can extend over 360° in the horizontal plane, which is the predominant visual plane. The field of each eye is approximately 177°. In a lightly anaesthetized cuttlefish the visual fields of the two eyes overlap anteriorly, to give a binocular field of 9 to 10°, but in life a considerably greater anterior overlap can be achieved (about 75°); there can also be an overlap posteriorly.

In Fig. 1 the optical axis is shown; it is defined as the line passing through the centre of the lens and the centre of the retina in the horizontal equatorial plane. As measured from photographs of dissections of freshly killed *Sepia*, the optical axis subtends an angle of between 76° and 90° to the body axis (cf. Heidermanns' (1928) value of 70°). With the living animal it is not so easy to define the optical axis precisely, and from projected single frames of 16-mm film measurement of the position of the eye is only accurate  $\pm 3^\circ$ . The optical axis can be defined approximately by measuring the position of the pupil: from such estimates the axis may lie between 70° and 90° when there is no prey in the visual field. These figures are provided as a basis for estimating the change in position of the eyes during attack; we shall take the average resting value of the optical axis as 80°.

Figure 1 also defines the terms *anterior* and

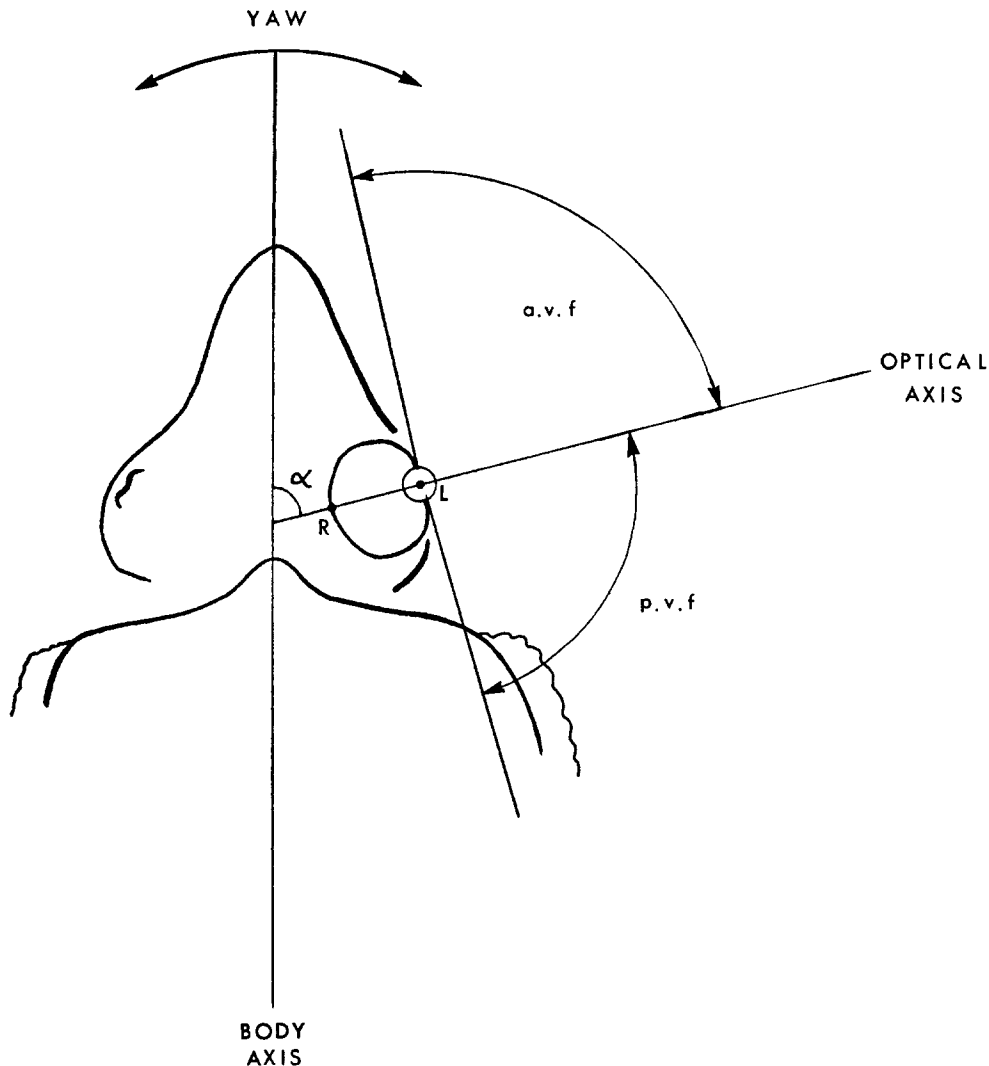


Fig. 1. Diagram to define terms used in the text. The head and eyes are viewed from above. The optical axis passes through the centre of the lens (**L**) and the mid-point of the retina in the horizontal plane (**R**). The angle it makes with the body axis ( $\alpha$ ) is between  $70^\circ$  and  $90^\circ$ . The horizontal visual field can be divided into an anterior (a.v.f.) and posterior visual field (p.v.f.), with respect to the optical axis. Movements in the horizontal plane about a vertical axis constitute *yaw*, for the eye as for the head and body.

*posterior visual field*. It will be shown that, although *Sepia* responds to stimuli in the posterior visual field, it only attacks prey that lies in the anterior visual field so that it re-positions itself preparatory to the attack.

### Results

*Sepia* generally captures fast-moving prey (e.g. prawns and fish) with the long tentacles;

slow-moving prey (e.g. crabs) may be seized with the arms alone.

### 1. The Attack on Prawns

It is convenient to recognize three components of the attack, which I propose to term: attention, positioning, seizure. The first and last terms are those used by Sanders & Young (1940) but the term 'positioning' is introduced as preferable

to their term 'approach', for in some cases the cuttlefish may remain at the same distance from the prey, or may even *retreat* before the final act of seizure is made.

**Attention.** When a prawn is introduced into the visual field of a hungry cuttlefish, the cuttlefish responds at once with a series of co-ordinated but clear-cut responses. The eye or eyes move, colour changes occur on the arms, head and mantle, the head and the body turn and the first, and sometimes the second, pair of arms are extended vertically upwards and perhaps waved from side to side. Generally the colour changes occur simultaneously with the eye movement; they persist throughout the turn that the whole animal makes, and continue after the erection of the arms. This phase of the attack may occupy less than 1 sec, or it may last for up to 10 sec.

The eye movements are in the yawing plane. The stimulated eye moves in such a direction that the image of the prawn is moved *towards the posterior region of the retina*. The unstimulated eye does not generally move at this stage but it may move so that the optical axis is inclined towards the prey. The eye movements precede movements from the head and body. The head turns towards the stimulated side and then the whole animal turns in the same direction, so that the angle between the body axis (Fig. 2 a, b) and the prey axis is reduced to zero and the head faces the prey. The image of the prey now lies on the posterior half of the retina, not only of the stimulated but also of the unstimulated eye, which has meanwhile also turned forward. The prey subtends approximately the same angle

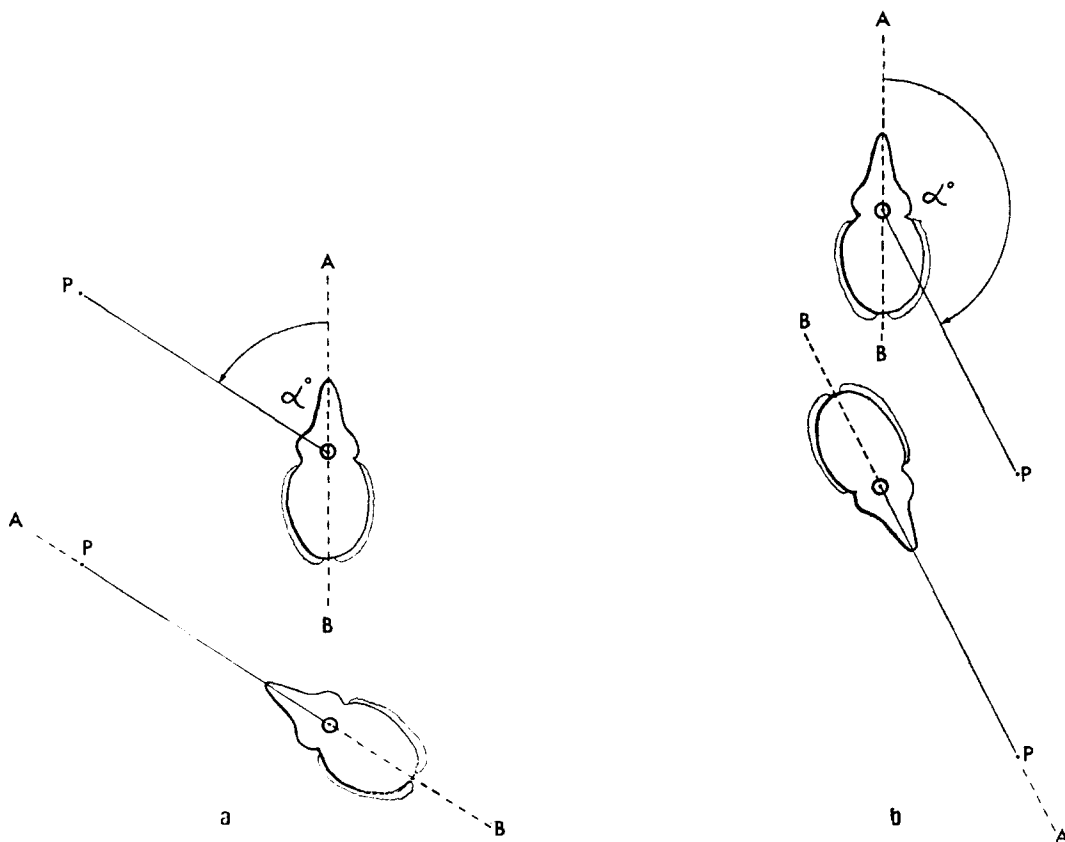


Fig. 2. Diagram of the behaviour during attention. The animal yaws so that the body axis (AB) and the prey axis (PO) become coincident. The animal may yaw through a few degrees or by nearly 180° during fixation.

to the optical axis of each eye (Fig. 3). The angle that the optical axis of the eye now makes with the body axis varied between  $38^\circ$  and  $66^\circ$  with a mean of  $52.5^\circ$  for fifteen different animals, whereas previously it was about  $80^\circ$ . Both eyes have therefore yawed in an anterior direction, i.e. there is *ocular convergence*. Several hundred attacks have been observed in the laboratory: these were *always* 'binocular'; in *Octopus* the attack is predominantly 'monocular' (Messenger 1967b).

The posterior visual field is considerable. Thus the angle ( $\alpha$ ) through which the cuttlefish yaws prior to fixation may be nearly  $180^\circ$  (Fig. 2b). The animal turns quite quickly about its own axis using the fins and funnel; in one typical sequence the turn through  $168^\circ$  took 1.51 sec. In another the turn through  $90^\circ$  took 0.75 sec.

The colour changes during this stage have been described by Holmes (1940). Waves of darkening pass over the body and arms; there

is a tendency for the raised arms to remain dark and occasionally the animal may show a strong mottling over the whole of the body and arms.

Sometimes in attention only the head and eyes turn. In this case the body axis will *not* be coincident with the prey axis, but the prawn will still subtend equal angles to the two eyes.

If, after the cuttlefish has assumed the attention position, the prey moves across the prey axis the cuttlefish also moves, so as to keep the prey and body axes coincident (Fig. 4). By moving a prawn in the visual field it is even possible to cause a cuttlefish to turn through  $360^\circ$  in the yawing plane to keep the prawn fixated.

Further evidence that the attack is visually induced can be gained by placing prawns in a glass tube in the aquarium, or by placing them in an adjacent aquarium, which may be as much as 30 cm away. The cuttlefish will go through all

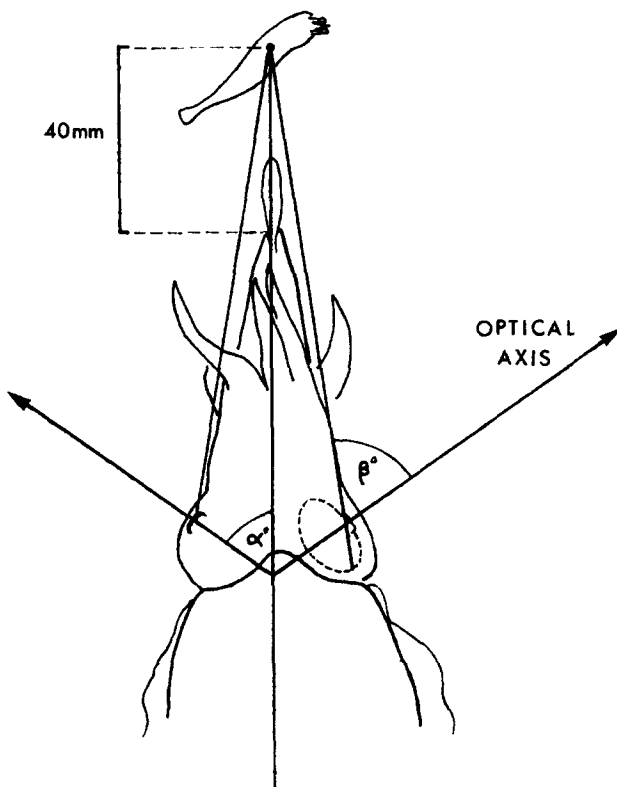


Fig. 3. Tracing from a projected 16-mm film frame at the moment of tentacle ejection. The optical axes now converge, the value for  $\alpha$  being  $54^\circ$ . The angle  $\beta$ ,  $68^\circ$ , is a measure of the position on the retina of the image.

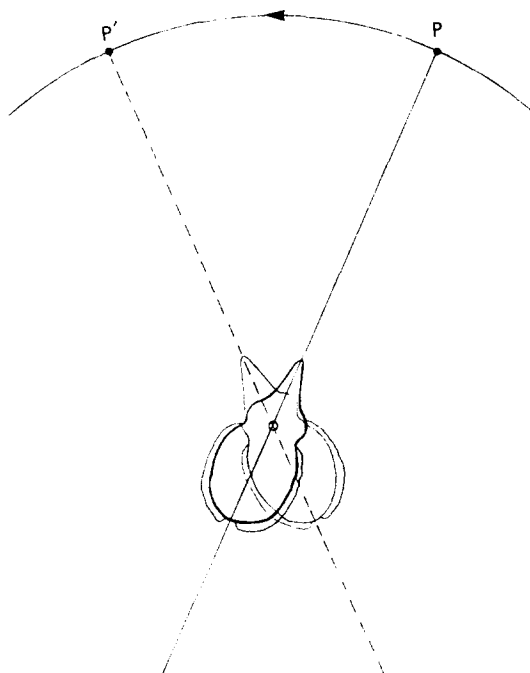


Fig. 4. Diagram to show how movement of the prey across the visual field (P to P') is followed by the whole animal yawing to maintain the fixation.

the attention stages of the attack. Similarly, as Wilson (1946) also recorded, cuttlefish sometimes attack reflected images in the glass of their tanks.

Freshly killed prawns, placed in the visual field, do not generally elicit attention movements; if the attention response is made it quickly fades and the later stages of the attack are not entered upon. Yet a prawn removed from the cuttlefish that has just captured and paralysed it will be attacked again if it is re-introduced into the tank immediately even though it lies motionless. Evidently objects tasted can be visually recognized.

After bilateral blinding every component of attention and, of course, the later stages of the attack are completely abolished. Four animals were operated in this way; two survived for 1 day only. The other two survived for over 2 days, after which they were killed off. All four animals became darkly mottled after recovery, and this was maintained by the two survivors until they were killed. Although they never responded to live prawns they accepted freshly killed prawns presented to the oral surface of the arms and dealt with them in the usual way.

Blind *Sepia* do not react to the sort of chemical stimuli that octopuses respond to (Wells, 1963a) so that juice from freshly killed prawns or crabs does not elicit any response from the animal if it is pipetted into the water a few mm away from the arms, head, eyes or 'olfactory' organ (Messenger, 1967c). There is therefore no evidence that *olfactory* cues are involved in the attack on prawns.

After unilateral blinding cuttlefish recover well, but their behaviour differs in that they respond only to objects in the field of the intact eye. Furthermore the tendency to attack falls off very strongly, not only when compared with intact *Sepia* but also *Sepia* that have undergone other types of operation (Table I). The first or

Table I. Number of Attackers per Group

Group	No. of animals	Percentage that attacked
1. Intake I (spring, white tanks)	15	80
2. Intake II (autumn, grey tanks)	36	75
3. Unilaterally blinded	29	34.5
4. First pair of arms removed	4	100
5. Unilateral tentacle removed	8	100

Groups 1 and 2 are day groups, as brought in from the sea. Groups 3, 4 and 5 contain animals that had attacked prawns in the aquarium prior to operation.

attention phase of the attack is therefore seen only rarely. Generally a lure prawn is not responded to at all although there may be eye movements alone. When the *Sepia* does respond, however, all stages of attention are similar to those in an intact cuttlefish. The animal turns so that prey and body axes are coincident and so that the angles subtended to the 'seeing' eye and the blind eye are approximately equal. If the prawn is moved across the visual field, the unilaterally blind preparation follows it, as does an intact cuttlefish.

The erection of the first and perhaps the second pair of arms is a most striking feature of attention. The first pair of arms generally adopt an S-shape and, keeping a few mm apart, are slowly waved from side to side at a frequency of approximately 0.5 per sec. Generally their aboral surfaces are very dark. The arms are also

commonly held in a V, and the second pair of arms—also dark—may adopt a similar posture. It is often held that these arms represent some form of lure. In a large cuttlefish their tips may be over 40 mm above the level of emergence of the tentacles and just as the colour changes themselves may act to distract the prey from the tentacles (Holmes, 1940; but see Wilson, 1946) so may the movements of the arms. If the first pair of arms is amputated the attention behaviour remains unaltered; the stumps of the amputated arms are raised and waved and other components of this phase are normal.

There is one report in the literature (Wickstead, 1956) that *Sepia* may use its *tentacles* as a lure—waving them from side to side. This has not been observed here—perhaps the species was not *S. officinalis*.

Tentacle removal (unilaterally or bilaterally) does not affect the behaviour at this stage of the attack, which is concluded in the usual manner.

Cuttlefish kept in total darkness for several hours did not capture prawns left in their tank and when observed in dark red light (Kodak Wratten filter No. 2) for several minutes they did not show attention. Yet after switching on a yellow light (or Wratten 1<sup>A</sup> light red filter) attention followed within 5 sec and, subsequently, positioning and seizure ensued.

**Positioning.** After the cuttlefish has turned so that it faces the prey, it may remain where it is, or approach or retreat along the prey-body axis. The approach is the most usual reaction and the cuttlefish may move as much as 70 cm before it pauses again about 8 cm from the prawn. If the prawn is very close to the animal (less than 5 cm) the cuttlefish will swim backwards until the tips of the arms are about one mantle-length (8 to 10 cm) away from the prawn. This is the sort of range—or *attacking distance*—over which cuttlefish of 9 cm attacks, but from first measurements it is clear that it is not a constant distance for any individual and Table V shows—in one animal making three attacks—how the attacking distance varies, and with it the degree of convergence of the eyes, an important clue to the mechanism of prey localization. Further investigations are now being made (Messenger, in preparation) to clarify this.

If, after the *Sepia* has yawed round to fixate the prawn, the latter already lies about 8 cm away on the prey-body axis, then it will enter the final stage of the attack without moving along the prey-body axis.

During positioning the first pair of arms remain erect and, perhaps, move from side to side. The second pair of arms may also be held up in a V. The fourth pair of arms are spread laterally, simultaneously flattening somewhat. The third pair of arms open slightly and from between them emerge the pale tips of the tentacles (cf. Wilson, 1946, Plate VII, Fig. 1). The tentacles are applied closely to each other. They protrude slowly and may be withdrawn and re-extended several times. Sometimes the tentacles may move from side to side over an arc of up to 10° in the horizontal plane. Such movements are also seen when the prawn moves a short distance transversely, the tentacles tending to follow the movement of the prey. At this stage the tentacles are extended only about a third of their full length, and they are evidently still under complete motor control from the inter-basal lobes (Boycott, 1961). The duration of this stage varies greatly: it may be over in less than 1 sec or may last for more than 10 sec. In one sequence, measured from ciné-film, it lasted only 0.33 sec, attention having lasted 1.5 sec and seizure lasting about 0.18 sec.

If the prey moves more than 2 to 3 cm at any time up to the end of positioning the cuttlefish withdraws its tentacles and realigns itself, if necessary returning to the beginning of attention. If the movement is along the prey axis the cuttlefish moves backward or forward appropriately.

If the prey is inaccessible, behind glass, the positioning behaviour remains the same in all its stages. Furthermore, if the prey behind glass moves the cuttlefish also moves in an attempt to maintain the optimum position for seizure. If cuttlefish and prawn occupy adjacent aquaria, the cuttlefish may swim into its glass wall in an attempt to reduce the distance between itself and its prey. It does not eject its tentacles yet, either fully or partly, suggesting that the whole attack is sequentially ordered, and that some form of distance perception operates.

Neither unilateral blinding, nor removal of the first pair of arms affects the behaviour at this stage of the attack, which is concluded in the usual manner. Similarly if the tentacles are removed (unilaterally or bilaterally) the behaviour is unchanged.

If the cuttlefish has been kept in the dark before this stage, it is not entered upon; if the light is interrupted during this stage the attack ceases.

**Seizure.** The transition from the last stage is an all-or-none phenomenon. The tentacles may remain for several seconds partly extended, pointing along the prey axis. The first pair of arms continue to be erect and wave from side to side. Waves of darkening may sweep over the upper sides of the arms, head and body. The rate of fin beat increases so that the cuttlefish seems to be hovering on the spot. Suddenly the whole animal jumps forward about 2 cm and the tentacles are launched at the prey and retracted so rapidly that film-analysis is necessary to analyse their behaviour. As the tentacles are ejected they are close together and parallel. The ends of the tentacles strike the prawn and *continue to travel forward, carrying the prawn away from the animal*. This is a feature of all the attacks studied and in some cases the prawn may be carried forward by nearly 100 per cent of the attacking distance. The tips of the tentacle reach the prawn in less than 32 msec (i.e. within 2 frames of ciné-film at 64 frames per sec); they then carry the prawn forward for another 60 to 75 msec at a reduced velocity, presumably because of the load. When the tentacles strike the prawn they flex in the central region and may even be thrown into folds. The shafts of the tentacles may cross distally at the moment of full extension, perhaps because of the flexure of the prawn in their grasp. Sometimes the ends of the tentacles bow and separate, while the shafts remain straight, but it is not clear whether or not this is because they have struck the tank.

This phase of the ejection lasts 30 to 75 msec and is followed by a pause of about the same duration. As withdrawal begins the curvature in the tentacle-shafts disappears until they again become straight, parallel and separated by only a few millimetres. The prawn is now steadily drawn towards the open ring of reflexed arms until it disappears. Complete withdrawal lasts from about 150 to 320 msec.

It will be shown below that in more than 80 per cent of instances *Sepia* captures the prawn first time. When it misses the prawn, the arms continue forward in just the same way and have to be completely withdrawn into the tentacular sacs before subsequent ejections are possible. Wilson (1946) has an excellent photograph showing how the tentacle is thrown into folds when it strikes the ground after missing a prawn, but our ciné-films show that this also occurs in successful attacks.

**The accuracy of the attack.** This was compared in two groups of animals, naive to laboratory

conditions (see *Methods*). The results are shown in Fig. 5. It will be seen that in both groups the accuracy of attack on prawns is very high. In the white tanks 81 per cent of animals captured prawns first time; 94 per cent caught them in two attempts or less. In the grey tanks 91 per cent of animals captured prawns first time, and 98 per cent caught them in two attempts or less.

What relation these scores bear to the performance in the sea is not easy to estimate. In natural surroundings prawns would be less conspicuous than in the tanks, either because of their coloration or because they tend to bury themselves in sand, though Verwey (quoted by Tinbergen, 1951) describes how cuttlefish flush them out. Once detected, however, they are probably caught as easily as in the laboratory for the illumination here—especially in the white tanks—must be brighter than anything *Sepia* encounters in life. One effect of this would be to close the iris, and the stopping-down thus obtained must increase the depth of focus and perhaps make the estimation of distance more difficult. In this connection it is interesting that the second group of cuttlefish, kept in grey tanks, made significantly fewer errors than the group in the white tanks, where reflected light was higher. (The groups are not strictly comparable however, for they were taken in the autumn and spring respectively.)

Failure to capture a prawn at the first attempt was usually followed by a successful second attempt or a subsequent successful attack (Table II, group A). Some animals gave up attacking without capturing prey (Table II, group B) and these were more likely to do so after two attempts than after one and never continued to make unsuccessful attacks: such animals were generally moribund and their results are not included in Fig. 5. In the open sea, of course, a prawn missed first time must have a greater chance of escaping capture a second time, even though *Sepia* can pursue objects that have left its visual field (Sanders & Young, 1940), so that in this respect the experimental situation favours the predator.

By presenting the cuttlefish with a prawn on a thread it is possible to move the prey at the moment that the arms are ejected. The prawn will then be missed and it is possible to withdraw repeatedly a prawn from a cuttlefish that had previously been scoring 100 per cent accurately. From this it is clear that the cuttlefish *aims* prior to ejection of the tentacles and the aiming



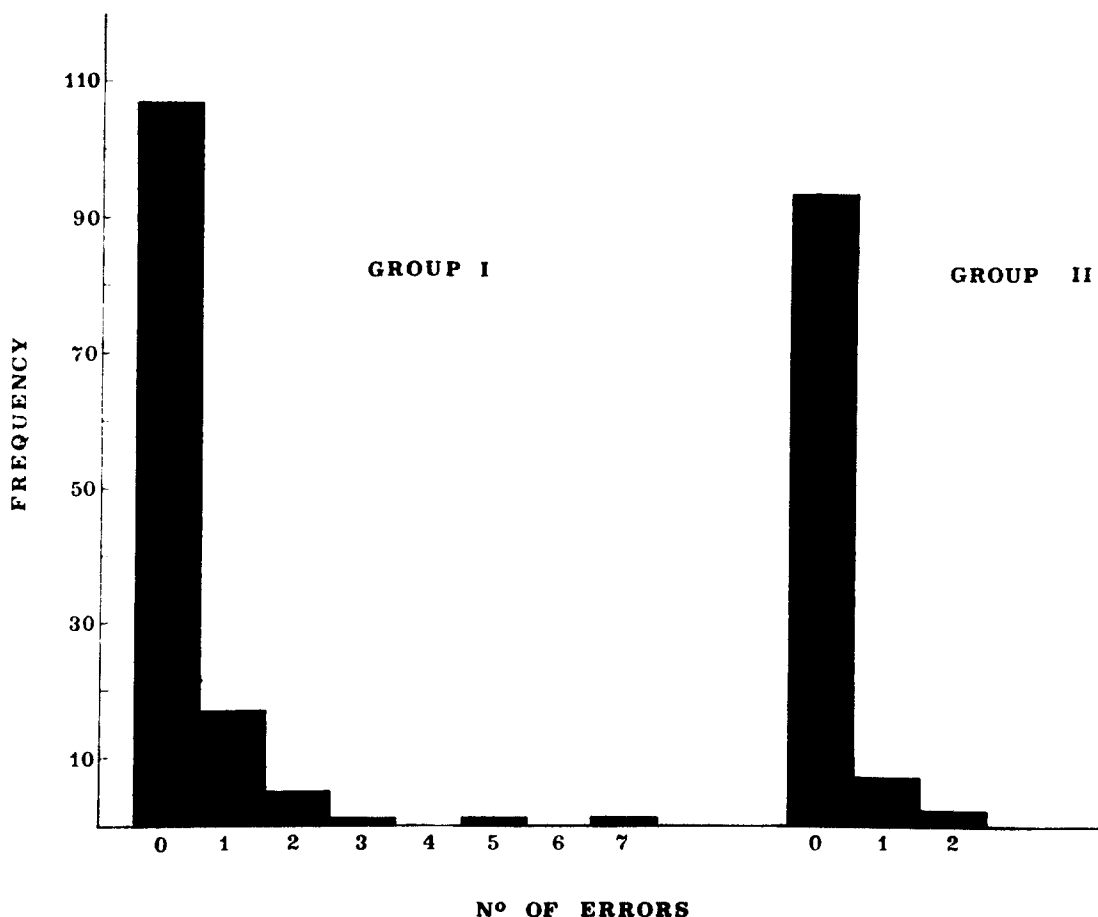


Fig. 5. Histogram showing how, in two groups of animals, the majority of attacks succeed without error. Group I: twelve animals in white tanks, spring; Group II: twenty-seven animals in grey tanks, autumn. The accuracy of attack was significantly higher in group II ( $\chi^2 = 5.78$ ,  $P < 0.05$ ).

programme cannot be re-set if the prey is subsequently moved; the control system is an 'open loop' one. Generally, failure to capture a prawn in the laboratory results from the movement by the prawn at the moment of the ejection. Indeed Wilson (1946) suggests that the prawn watches the tentacles until the last moment and then moves.

If the prawn is behind glass the tentacles are ejected in the usual way and strike the glass very strongly. They are then withdrawn, often with difficulty, and the ejection repeated when the other stages of the attack have been completed and when the prawn is the usual 8 to 10 cm away. If the prawn behind the glass is further away seizure is not attempted.

If the cuttlefish is unilaterally blinded the

final stages of the attack are as in intact cuttlefish but the accuracy of attack falls to about 56 per cent (Table III, Fig. 6). Examination of the shots that missed failed to establish a common type of error. Either the direction or—more frequently—the distance was inaccurately estimated. On present evidence it is not clear how such a monocular attack was so accurate though probably *Sepia* only estimates the *direction* of its prey and not the distance (see *Discussion*); additional data are being collected.

Removal of the first pair of arms from four *Sepia* shows that whether or not they function to distract the prawn during the early stages of the attack, a cuttlefish can still successfully capture prawns without them (Table III). Indeed in the sample chosen the score was

Table II. Effect of Failure on Subsequent Attacks in Two Groups of *Sepia*

Attack failed at the	Group A	Group B	
	No. that failed	No. that failed	No. that then ceased to attack
1st attempt	34	14	6
2nd attempt	10	8	7
3rd attempt	1	1	1
4th attempt	0		
5th attempt	1		
6th attempt	0		
7th attempt	1		

Group A comprises groups I and II (Table I), thirty-nine animals in all.

Group B comprises animals not included in groups I and II because they failed to capture prawns. They were generally damaged animals, and died.

slightly higher after operation than before.

The removal of one tentacle does not affect the act of seizure qualitatively but, as might be expected, the attack is less often successful (Table III): only 63 per cent of attacks were successful first time. Nevertheless 82 per cent of attacks were successful at the first or second attempt and this level of success is testimony to the effectiveness of the sucker as a grasping device, as well as to the accuracy of the shot. It also shows that the tentacles need not be used together, like tongs, to capture prey (cf. *Ommastrephes*, Clarke, 1966).

After bilateral tentacle removal the early stages of the attack are completed as in intact cuttlefish but the final stage is marked only by a sharp lunge forward by the whole animal, through 2 to 3 cm. This brings the tips of the arms about 5 to 8 cm away from the prawn, so that the attack is not rewarded. This behaviour may be repeated, up to twenty times in 30 sec: only after repeated presentation over several days does the forward lunge—associated in the intact animal with tentacle-ejection—disappear and even then all the components of attention and positioning are passed through.

If the lights are turned off at the moment the tentacles are ejected the attack is still successful, suggesting again that prior to seizure the cuttlefish has estimated the position of its prey in space (cf. Maldonado, 1964).

## 2. The Attack on Crabs

Wilson (1946), Boycott (1958) and Boulet (quoted by Wells, 1962) all point out that cuttlefish catch crabs—presumably another common prey—in quite a different way. The crab is 'jumped on' and seized by the arms; the tentacles are not ejected. A cuttlefish that jumps on a crab goes through the first two stages of the attack sequence as if it were attacking a prawn; it turns, so that the crab subtends the same angle to each eye, pauses at about 8 to 10 cm from the crab, generally keeping above it, and finally lunges forwards and downwards.

None of the workers cited above records that a cuttlefish *may* capture a crab with its tentacles. After this had been observed once or twice in the aquarium the frequency of the two forms of attack was measured in three groups of cuttlefish (Table IV). In total, tentacle attacks prevailed over arm attacks (64 per cent: 36 per cent), but from the table it is clear that there are large variations between individuals, presumably as a result of their different past experience.

The same authors also report that *Sepia* commonly 'stalk' around a crab and so position themselves that the forward lunge of the last stage of the attack is directed at the back of the crab. This sort of behaviour does occur but by no means invariably, and for the size-range of crabs tested (20 to 80 mm carapace width) the *Sepia* is just as likely to attack head-on, if it attacks at all. The suckers on the arms are so effective at immobilizing the crab that such a frontal attack is feasible. Sometimes the crab is turned by the arms so that the chelae are held outwards away from the body. In any case the crab is rendered harmless in about 7 to 8 sec (see below).

In the Naples aquaria young *Sepia* have also been observed feeding on fry (*Mugil* sp.), which they capture with the tentacles; and once a *Squilla* was seized by an adult with its arms. On two separate occasions, a small *Sepia* (20 mm) left in the same tank as a large one (c. 100 mm) disappeared within hours. The method of attack was not observed.

## 3. Disposal of Prey

By allowing *Sepia* to capture a prawn on a thread, and subsequently withdrawing it, it is possible to show how the prey is dealt with. The prawn is transferred to the mouth and bitten on either side of the abdomen near its point of flexure (Wilson, 1946); sometimes a wedge of flesh is removed from the dorsal side,

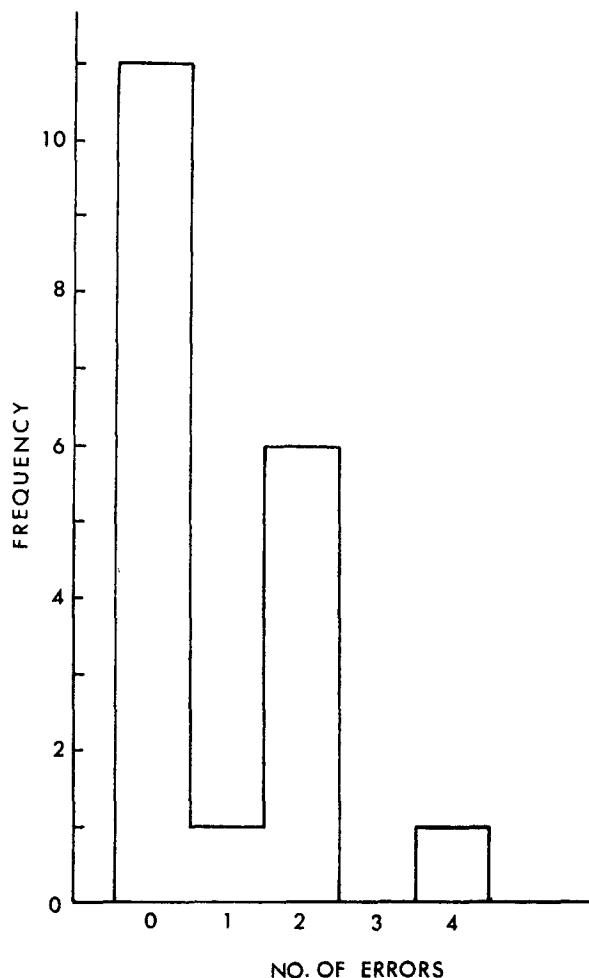
Fig. 6. Histogram of attacks by unilaterally blind *Sepia*.

Table III. Accuracy of Seizure After Various Lesions

	Unilateral blinding	Removal of 'lure' arms	Unilateral tentacle removal
Number of animals	8	4	7
Mean % of shots successful first time	56	90	63
Mean % shots successful first or second time	59	100	82

Table IV. Two Types of Attack on Crabs

Group	Number	Tentacle attacks	Arm attacks
A	12	8	6
B	17	26	13
C	14	14	8
Total		48	27

N.B. All animals were tested in grey tanks.

and once the head was found to have been bitten off. The bite is administered rapidly and prawns withdrawn from the mouth after 5 sec or more after capture are already moribund or dead.

Similar or even larger cuts with scissors do not cause such rapid death and it is clear from this—and from the behaviour of moribund animals—that death results from poisoning of the

nervous system. The limbs of prawns withdrawn at 5 to 6 sec are convulsive, and remain so for a few seconds before death ensues.

Crabs are dealt with similarly but if removed within 9 sec may recover. Again the limbs show convulsions and the behaviour is consistent with poisoning, probably by cephalotoxin from the posterior salivary glands (Ghiretti, 1960). No trace of a wound in the carapace has been found in crabs recovered from cuttlefish. Is the poison sprayed into the branchial cavities by the salivary palp?

Prawns are devoured almost entirely, only the antennae and rostrum being discarded, but the whole carapace, the chelae and the walking legs of crabs, may be left by the cuttlefish (cf. Bidder, 1966).

*Sepia* in the size-range 80 to 120 mm take five or six prawns (55 to 63 mm) a day in temperatures from 15° to 25°C. They may be taken one after the other at intervals of less than half a minute, or will be accepted at longer intervals throughout the day. In neither case is it possible to increase the food intake significantly. One or two crabs (carapace width 20 mm) are taken daily in the aquarium, but it seems likely that in the sea the intake of the food might be greater for the growth rate is very rapid in *Sepia* (Packard, 1966; Denton & Wilson, quoted by Denton & Gilpin-Brown, 1966).

Operated animals deal with prey in the way described: bilaterally blinded animals accept prey if presented to the arms. Operated animals maintain the same level of food intake as unoperated animals, but unilaterally blind animals commonly starve (see above).

#### 4. The Eyes

**Eye movements.** It is convenient to recognize two categories of eye movements (Davson, 1963). First, visually induced *fixation movements* and secondly, non-visually induced *orientation movements*. Both types of movement occur in *Sepia*, whose eyes possess elaborate extrinsic eye muscles (Glockauer, 1915).

In *Sepia* there are *fixation movements* in the horizontal plane. The movements of the eyes described above for the first two stages of the attack clearly fall into the first category. They occur while the cuttlefish is stationary—i.e. when there can be no changing information from the statocysts—and they can be made to recur if the prawn is moved. Indeed, if the prawn is moved around the animal the eyes move in the *same direction* before the animal turns to follow. The movements of the eye and the animal

always tend to shift the image of the prey to the back half of the retina, suggesting that here is an area of special vision. From tracing projected frames of ciné-film of several attacks it is possible to show that the angle subtended by the prey to the optical axis lies around 70° at the moment of fixation (Fig. 3). The so-called *fixation axis* thus appears to be constant (within the limits of our technique) so that for the first time in cephalopods we have evidence that the image of the prey is always localized on one part of the retina at the moment of attack. (Packard (personal communication) has some data on the *Octopus* attack showing that the prey image is generally brought onto the back half of the retina of the attacking eye.) It has been found that the fixation axis is about the same for both eyes (Fig. 3), that is binocular convergence obtains during the attack. Even more striking, it seems that the degree of convergence of the eyes increases as the attacking distance diminishes (Table V). Furthermore unilaterally

Table V. Relation of  $\alpha$  to attacking Distance in a Single Individual

Attack	$\alpha$	Attacking distance
1.	47°	81.9 mm
2.	54°	99 mm
3.	58°	104 mm

blind *Sepia* adopt an identical attacking position that would again bring the image on to the back half of the retina. Is this evidence that this is an area of specialized vision, a kind of 'area centralis'? Young (1963a) found that the retina of *Sepia* is not anatomically uniform. The rhabdomes are longer and more closely packed in a horizontal strip lying along the equator of the eye, and in these rhabdomes the rate of pigment migration, during light- and dark-adaptation, differs from other regions in the eye. Furthermore there are two specialized regions within the strip, one anterior and the other posterior, the rhabdomes being especially closely packed in the latter, more than 100,000 per mm<sup>2</sup>.

In the most usual attack situation in the laboratory the *Sepia* and prawn lie on the bottom of the tank, so that the image of the prawn on the retina must lie on or near Young's equatorial strip. The movements described here move the image along this strip towards the posterior end. It is noteworthy that when the

prawn is much above or below the cuttlefish the latter attacks with its eyes tilted (anterior margin up or down, respectively) in the vertical plane, so that again the image must lie on the equatorial strip during the attack.

Further experimental evidence is needed to make certain that this region of the retina is an area of specialized vision but the way in which the image of the prey is consistently moved there during fixation makes it very likely.

Horizontal eye movements can also be obtained by placing the cuttlefish at the centre of a revolving striped field, though not a revolving plain background (Messenger, unpublished observations). Such movements are the well-known *nystagmus*, comprising a short 'flick' and a long 'drift' component, the latter occurring in the same direction as the movement of the field. If the drum rotates in the clockwise sense the eyes will 'drift' to the right. These movements need not imply that there is an area of special vision but they are clearly visually induced; it is interesting that nystagmic movements cannot be elicited by vertically moving stripes, i.e. by a drum revolving about a horizontal axis, for vertical eye movements have never been observed in the aquarium. That the eye movements seen in the aquaria and in the striped drum are always in the horizontal or yawing plane emphasizes that this is the predominant visual plane of the animal.

There is evidence from two sources about *orientation movements* in *Sepia*. First (Messenger, unpublished observations), the eyes of *Sepia* are always horizontal and remain so while the body of the animal inclines in the pitching plane, if the background is uniform. If the animal is fixating its prey, however, *the horizontality is overcome*, as described above, presumably to hold the image on the equatorial retinal strip. (cf. *Octopus*, where Wells (1960) has reported that the horizontality of the pupil is apparently constant.) Secondly, Dijkgraaf (1963) reported after-nystagmic movements of the eyes, in the horizontal plane, when rapid deceleration was applied to a cuttlefish rotating within a plain background. This has been confirmed here.

**The pupil.** In *Sepia* the pupil is W-shaped, and in very bright illumination the iris will close so much that the central part of the W is occluded and two separate pupils are formed. This is evidently related to the possession of anterior and posterior specialized retinal areas (Young, 1963a) though in what way is not clear. In the laboratory the prey is always viewed

through the anterior pupil during fixation so that its image would fall in the posterior half of the retina.

The iris opens wide as illumination decreases, ultimately becoming fully circular, but it can also change shape during constant illumination. When an object vertically above the eye moves over towards the midline of the animal, the iris opens up fully, moving up like a blind, presumably to keep the image on the retina.

## Discussion

### The Binocular Attack

From the evidence presented it is clear that the attack by *Sepia* is initiated and maintained by visual cues alone. Moreover it is shown that the fixation is always binocular. This contrasts with *Octopus*, where attacks occur when the image falls on one eye alone. Although octopuses can attack so that the prey remains in the visual fields of both eyes during the 'jump' forward (Messenger, unpublished observations) and although Packard (personal communication) has also recorded backward 'binocular attacks', these are unusual in the laboratory.

This difference between the two genera relates to their feeding habits and mode of life. *Sepia* seizes small fast-moving prey with an all-or-nothing 'stabbing' device that requires accurate spatial location. *Octopus* jumps onto crabs and envelops them with the outspread web and arms. Although the octopus aims before launching its attack (Maldonado, 1964), the form of the animal and its mode of descent onto prey means that a considerable margin of error can be tolerated. Hence relying on the restricted information derivable from one eye is adequate for an octopus. Moreover the independence of the two eyes is a feature of *Octopus* that is adapted to its habit in crevices and among rocks on the sea floor. It may sit in its 'home' so that only one eye is directed outwards or it may squeeze sideways through a crack; in either case a crab that enters the visual field of only one eye must elicit a rapid attack.

### Localization of the Prey in Space

Perhaps the most interesting aspect of the attack by *Sepia* is that it can estimate the position of its prey so accurately that over 90 per cent of its attacks succeed first time.

After the cuttlefish has positioned itself for seizure there are two ways in which it could locate a prey with its tentacles: (1) it could estimate exactly the *direction* and *distance* of the prey, or (2) it could determine the exact

*direction* only but not the distance which has already been taken approximately into account. In support of the first method is the finding that the eyes converge by an increasing amount as the attacking distance diminishes, so that if proprioceptive information from the eye muscles were available it could theoretically be used to relate distance to the amount of torque the eyeball has undergone. Furthermore after a 'monocular' *Sepia* has fixated its prey its head and body turn 'about the eye' in the usual way, suggesting that the position of the eye in the orbit is taken into account. However Wells (1963b) has repeatedly demonstrated in another cephalopod, *Octopus*, that proprioceptive information cannot be integrated with visual information at least in learning situations, and Brindley & Merton (1960) have conclusively shown that there is no position sense in the eye muscles of man, the only animal in which this has been studied. It seems unlikely, then, that the first method of localization operates in *Sepia*, though further experiments are needed before we can be sure of this.

In support of the second method is the finding that the tentacles are always ejected with sufficient force to carry them well past the actual position of the prawn—perhaps twice as far. When the prawn is captured, indeed, it is initially carried further away from the cuttlefish. This is at first sight rather surprising and it contrasts with another visually-programmed open-loop system—the jump of the lesser galago (Hall-Craggs, 1965)—where there is close agreement between the measured and theoretical take-off velocity that would just carry the galago to its perch. This system is nicely controlled to utilize the minimum muscular effort to gain a particular height.

If the cuttlefish comes within striking distance of the prawn—which from preliminary measurements always seems to be about one dorsal mantle length away—and aligns itself so that the prawn subtends equal angles to both eyes it has only to eject the tentacles directly in front of it to be certain of capturing the prawn, and the precise distance away that the latter lies need not be calculated.

Unilaterally blind *Sepia* are less accurate attackers (Fig. 6) than intact animals, but their errors are not consistent in type. Under-shooting is the commonest error but errors in direction also occur; the animals aim away from the intact side. The way unilaterally blind *Sepia* turn to bring the image onto the back of the remaining

retina confirms the idea that once the image is on the 'special area' the cuttlefish has only to eject its tentacles straight ahead. It seems likely, therefore, that normally cuttlefish locate the direction of their prey using information from the two eyes but that at this stage they do not accurately estimate its distance. This is unnecessary since the tentacles are always ejected straight ahead with sufficient force to pass beyond the prey's position, and *prior positioning has always brought the cuttlefish to within a tentacle length of the prey*. Presumably the size of the image on the retina is the critical clue here and it is noteworthy that *Sepia* separated from their prey by glass only eject their tentacles if the prey lies within tentacle length. Experiments are now being undertaken to investigate depth perception in *Sepia* but it is already clear that in the experimental tanks used, which did not provide a uniform background, cuttlefish were able to estimate depth monocularly; unilaterally blind cuttlefish still swam 60 to 70 cm down the tank in the positioning phase of the attack, whether the prawns were large or small.

#### The Control System for the Attack

The control of the attack falls into two phases. The first—comprising attention and positioning—is a visually-controlled closed loop system. Movement of the prey is followed by movement of the cuttlefish (Fig. 4), which reduces the visual error signal until it comes close to zero.

However, as in other pre-catching mechanisms (Mittelstaedt, 1957) the final phase (here: seizure) is so rapid (about 30 msec) that there can be no time for visual feedback about the position of the tentacles. The control system is therefore an open loop one, and the position of the prey must be estimated and a complete set of orders issued before the tentacles are ejected. Verification that this is so comes from experiments (a) that interrupt the light during the ejection when the prey is still captured, and (b) that move the prey during the ejection when it is missed. Whether visual information alone is used to programme the attack is not yet known; but it is possible that proprioceptive cues from the eye muscles are also used. If *Sepia* can correlate visual with proprioceptive information, this would constitute the first recorded instance in cephalopods of such an interaction (cf. Wells, 1963b).

#### The Two Attack Systems and Learned Behaviour

The development in decapod cephalopods

of a pair of arms specialized for seizing prey was presumably necessary to capture the fast-moving prey that they encountered in the ocean. Crustaceans, with giant-fibre systems, and fish, with myelinated nerves, could move so quickly that a mechanism for rapid seizure had to be developed. When *Sepia* reverted to the benthic habitat it encountered slow-moving prey that could be captured by the arms. This type of attack is presumably individually learnt as a result of experience and reference to Table IV shows that even in three very small samples the prevalence of one form of attack varies considerably.

Wells (1958) showed that newly hatched *Sepia* attack *Mysis* on the first occasion they are presented with the tentacles, and Boulet (quoted Wells, 1962) claimed that newly hatched *Sepia* always attack small crabs using the tentacles. It is interesting that *Sepia* deprived of tentacles do not attempt to capture prawns with the arms, though they do capture crabs that way.

The attack of cuttlefish without tentacles on free-swimming prawns partly habituates, i.e. the response of *seizure* wanes in the absence of reinforcement. One individual, for example, made twenty incipient 'shots' in the first half-minute it was shown a prawn. On the second trial, 24 hr later, it made only four shots and on the third trial 48 hr later none although it still went through the attention and positioning stages of the attack. Habituation has been described before in *Sepia* by Sanders & Young, (1940) and Wells (1958) in both cases to prawns behind glass. In such a situation the adult animal quickly learns to inhibit the ejection of the tentacles. The possibility that habituation is dependent on the reception of pain signals from the tentacles that strike the glass is less likely in the face of this new evidence. There is, of course, no inferior frontal-sub-frontal system in *Sepia* (Young, 1963b) so that this result is not altogether surprising, but it would be interesting to compare the relative rate of habituation in normal and tentacle-less cuttlefish to prawns behind glass.

#### Summary

1. The attack by *Sepia* on prawns comprises three phases: *attention*, *positioning* and *seizure*.

2. In attention there are colour changes, erection of the first and second pair of arms and movements of the eyes and head. The whole animal turns (by up to 180°) so that the prey comes to lie on a forward extension of the body

axis, subtending equal angles to the two eyes. The images now lie on corresponding areas in the two retinas: on the posterior part of the equatorial retinal strip.

3. During positioning the cuttlefish swims towards or away from the prey until it is about one mantle length away from it. This attacking distance (AD) is not constant per individual and measurements show that as the AD decreases so the degree of anterior ocular convergence increases.

4. In seizure the tentacles are ejected very quickly: the prey is seized within 30 msec by the terminal suckers and *carried further away* from the animal for another 60 msec before being drawn back to the mouth in about 150 to 300 msec. *Sepia* may seize slow-moving prey (e.g. crabs) with the arms alone, but in the sample tested tentacle attacks predominated. Prawns are bitten in the abdomen and poisoned rapidly: they are dead within 5 sec of seizure. Crabs die within 9 sec but it is not known how they are poisoned.

5. Experiments are described that show the attack is initiated by visual cues alone and that during attention and positioning visual information continues to control the attack (closed-loop control). The rapid nature of seizure precludes control by visual feed-back and this phase of the attack is under open-loop control. The accuracy of attack is very high in the laboratory (85 to 90 per cent attacks successful) first time. After monocular blinding the level of accuracy is 56 per cent. In cuttlefish with only one tentacle 63 per cent of attacks are successful first time.

6. Possible ways of achieving such precise aiming are discussed. It is proposed that the *direction* of the prey is estimated by comparing the image position in the two eyes: once the prey-image lies on the 'special area' on both retinas the tentacles can be ejected straight ahead. Once the cuttlefish is within AD the *distance* need not be accurately estimated for the tentacles are always ejected with sufficient force to carry their tips well past the prey position. However, it is not known how the animal calculates the AD: the size of the retinal image may be an important cue.

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