J. exp. Biol. ***191****, 247–256 (1994)*
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GRAVITY AND LIGHT INFLUENCE THE COUNTERSHADING REFLEXES OF THE CUTTLEFISH *SEPIA OFFICINALIS*

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Accepted 16 March 1994

Summary

Rotation (roll or pitch) of a cuttlefish away from its normal orientation produces countershading reflexes (CSRs) that consist of chromatophore expansion on the ventral body surface. When rotation is in the roll plane, the CSR has two components on each side of the body. The first (component A) consists of a unilateral expansion of chromatophores on the uppermost latero-ventral edge of the mantle, the underside of the upper fin and the uppermost side of the head; it occurs when the angle of rotation is less than 90°. Further rotation (from approximately 90° to approximately 180°) adds the second component (component B): a unilateral expansion of the chromatophores on the upper half of the ventral surface of the mantle, funnel, head and arms. When rotation is in the pitch plane, chromatophores expand on the posterior part of the ventral mantle and fins when the head is down; when the head is up, chromatophores expand on the ventral surface of the arms, head and funnel and on the anterior part of the ventral mantle and fins. The pitch CSR is always bilateral.

Destruction of the gravity or the angular acceleration receptor systems of the statocysts demonstrates that it is the gravity receptor systems that drive the CSRs. Unilateral destruction of the gravity receptor systems shows that the pitch CSR is driven bilaterally, whereas the roll CSR is driven unilaterally. Components A and B of the roll CSR are driven by input from the ipsilateral statocyst, but component A is additionally driven by light.

Brain lesions provide evidence that the pathways for the CSRs run through the lateral basal lobes in the supraoesophageal part of the brain.

Introduction

Many animals, including cephalopods, conceal themselves from predators and prey by

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Key words: statocyst, sensory input, chromatophores, countershading, camouflage, cephalopod, cuttlefish, *Sepia officinalis*.

countershading: the upper surface is dark while the lower one is light. This has the effect of making the body less obvious against the background when the illumination comes mainly from above (Thayer, 1909; Cott, 1940). In cephalopods, countershading is achieved mainly with chromatophores; those in the dorsal skin are more abundant and show more tonic expansion than those on the ventral surface. The pallor on the ventral surface is also due, in part, to large numbers of iridophores (see Discussion).

A unique feature of cephalopods is that their countershading is not permanently fixed. When a fish is turned upside down, it becomes very conspicuous because its countershading is fixed. In contrast, when a cephalopod is turned upside down, the chromatophores on the ventral side of the entire mantle, funnel, head and arms expand and those on the dorsal side retract. If a cephalopod is rotated about 90 ˚ in the roll plane, the chromatophores on the upper half of the body expand, while those on the lower half retract (Holmes, 1940). This response prevents the cephalopod from becoming conspicuous and has been termed the countershading reflex (CSR) (Ferguson and Messenger, 1991).

Such a reflex is possible because cephalopod chromatophores are expanded by radial muscles that are under direct neural control. Their motoneurones are located in the chromatophore lobes of the suboesophageal brain (Sereni and Young, 1932; Dubas *et al*. 1986). The chromatophore lobes are, in turn, controlled by 'higher' centres in the supraoesophageal brain, the lateral basal and optic lobes (Boycott, 1961; Young, 1971, 1976, 1977). In response to motoneurone activity, the chromatophore muscles contract, causing rapid expansion of the pigment sac (Florey, 1969; Florey and Kriebel, 1969).

In cephalopods, most colour changes are driven by visual input (Boycott, 1953, 1961; Packard and Sanders, 1971; Hanlon and Messenger, 1988). Previous experiments suggest, however, that the CSR is not driven visually but by sensory input from the statocysts: when they are destroyed, the reflex is abolished (Ferguson and Messenger, 1991). The cuttlefish *Sepia officinalis* has two statocysts, each containing two types of receptor systems: one for the detection of gravity (and other linear accelerations) and one for the detection of angular accelerations (Fig. 1). The gravity receptor system has three separate sensory epithelia (maculae), one covered with a compact statolith (MSP) and two covered with statoconial layers (MNI, MNS). The angular acceleration receptor system is subdivided into four sensory epithelia (cristae), each of which has a cupula attached to it (Budelmann, 1990).

The present paper describes the CSR in more detail and investigates, by selective destruction of the gravity and angular acceleration receptor systems, how the statocysts control the CSR of *Sepia*. Experiments using bilaterally blinded animals examine whether visual input influences the CSRs. Animals with brain lesions are used to determine the pathways by which the statocysts influence the chromatophore lobes.

Materials and methods

Experimental animals

Sepia officinalis (mantle length 75–110 mm) from the Gulf of Naples were maintained in an open seawater system at temperatures of 16–23 ˚C. In all, 36 animals were used, of

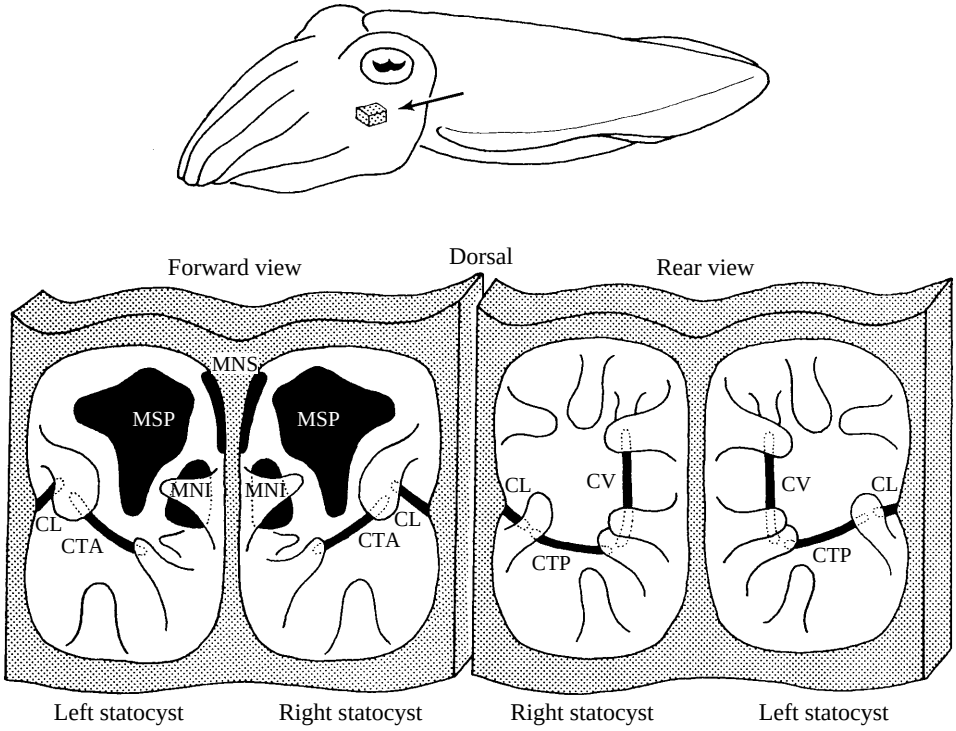

Fig. 1. The statocysts of the cuttlefish *Sepia officinalis* lie in the cranial cartilage underneath the brain (dotted area in top diagram). The lower diagrams show forward and rear views into the open statocyst cavities after a transverse vertical cut. Each cavity contains three gravity receptor systems (MNI, macula neglecta inferior; MNS, macula neglecta superior; MSP, macula statica princeps) and an angular acceleration receptor system, which is subdivided into four segments (CL, crista longitudinalis; CTA, crista transversalis anterior; CTP, crista transversalis posterior; CV, crista verticalis).

which 6 were left intact, 17 had surgery performed on the left statocyst, 2 had surgery performed on both statocysts, 2 were blinded and 9 received brain lesions.

Surgical procedures

Animals were anaesthetized either in a mixture of 50 % sea water and 50 % isotonic $MgCl_2$ (Messenger *et al*. 1985) or in a 1.25 % solution of absolute ethanol in sea water. Ethanol was used when the seawater temperature was above 22 ˚C, because the animals showed better and faster recovery (3 min *versus* 15 min).

Surgery was normally performed on the left statocyst; full procedures are given in Budelmann (1990). The gravity receptor systems were selectively destroyed: the statolith was removed from the MSP epithelium with fine forceps, and the statoconial layers were detached from the MNS and MNI epithelia by jets of sea water. To destroy the angular acceleration receptor system, the cupula was removed from each of the four crista segments with a hair crushed to form a fine brush.

To eliminate visual input (hereafter referred to as ‘blinding’), the eyes of two animals

were covered by disks of black polyethylene that had been moulded into cups. These were glued over the eyes (under ethanol anaesthetic) with Superattak (Loctite). Animals recovered well and showed no signs of stress or irritation (they did not try to remove the discs with their arms). No chromatic responses were elicited by discharges of a flash gun when the cups were in place, suggesting that the blinding procedure was effective.

To perform brain lesions, the skin and muscles overlying the dorsal surface of the cranium were cut under anaesthetic and an incision was made through the cranium to reveal the supraoesophageal brain. This was then removed either completely or unilaterally; in other operations, the lateral basal lobe was removed on the right side. The cranium was closed with sutures and the skin glued back in position using Superattak.

After surgery, animals were revived by perfusing their mantle cavity with sea water. Immediately after behavioural testing, the operated animals were killed by decapitation, and autopsies were performed to verify the success of surgery. The statocysts were opened and examined macroscopically to verify that statoconial layers and/or the statolith had been removed; scratches through the cristae ridges (caused by the hair brush) were taken as a sign of successful removal of the cupulae. Gross brain lesions were confirmed visually, but it was necessary to examine serial sections of brains (cut after paraffin embedding) to ensure that lesions of the lateral basal lobe had been successful.

Behavioural testing

Cuttlefish were rotated manually whilst held by hand or in a special holder. For easier handling, the animals were lightly anaesthetized with 0.4 % ethanol in sea water, which does not abolish chromatophore activity. Animals that had undergone statocyst operations were usually tested 30 min after surgery. Animals with brain lesions were allowed 24 h to recover before being tested. To test for the roll CSR, animals were rotated from their normal position (0 °) through approximately 90 ° (left up, then right up) or through approximately 180 °. To test for the pitch CSR, animals were rotated through approximately 90 °, to a position with the head either up or down. Care was taken to ensure that the chromatophores on the ventral surface of the body were in the retracted state before each test and that the head was not in an oblique position relative to the body. Individual tests were repeated at least five times. Responses were recorded with a S-VHS colour video system (Panasonic) and replayed for subsequent analysis.

Results

The countershading reflexes

The roll countershading reflex

When a cuttlefish is rotated onto its back (i.e. through 180 ° in the roll plane), chromatophores all over the ventral surface of the mantle, fins, funnel, head and arms expand; when it is rotated through approximately 90 °, the chromatophores expand only on the upper half of the ventral surface (Ferguson and Messenger, 1991).

The present experiments confirm the existence of this CSR in the roll plane, but they also show that the chromatophores of the ventral side are organized in populations or

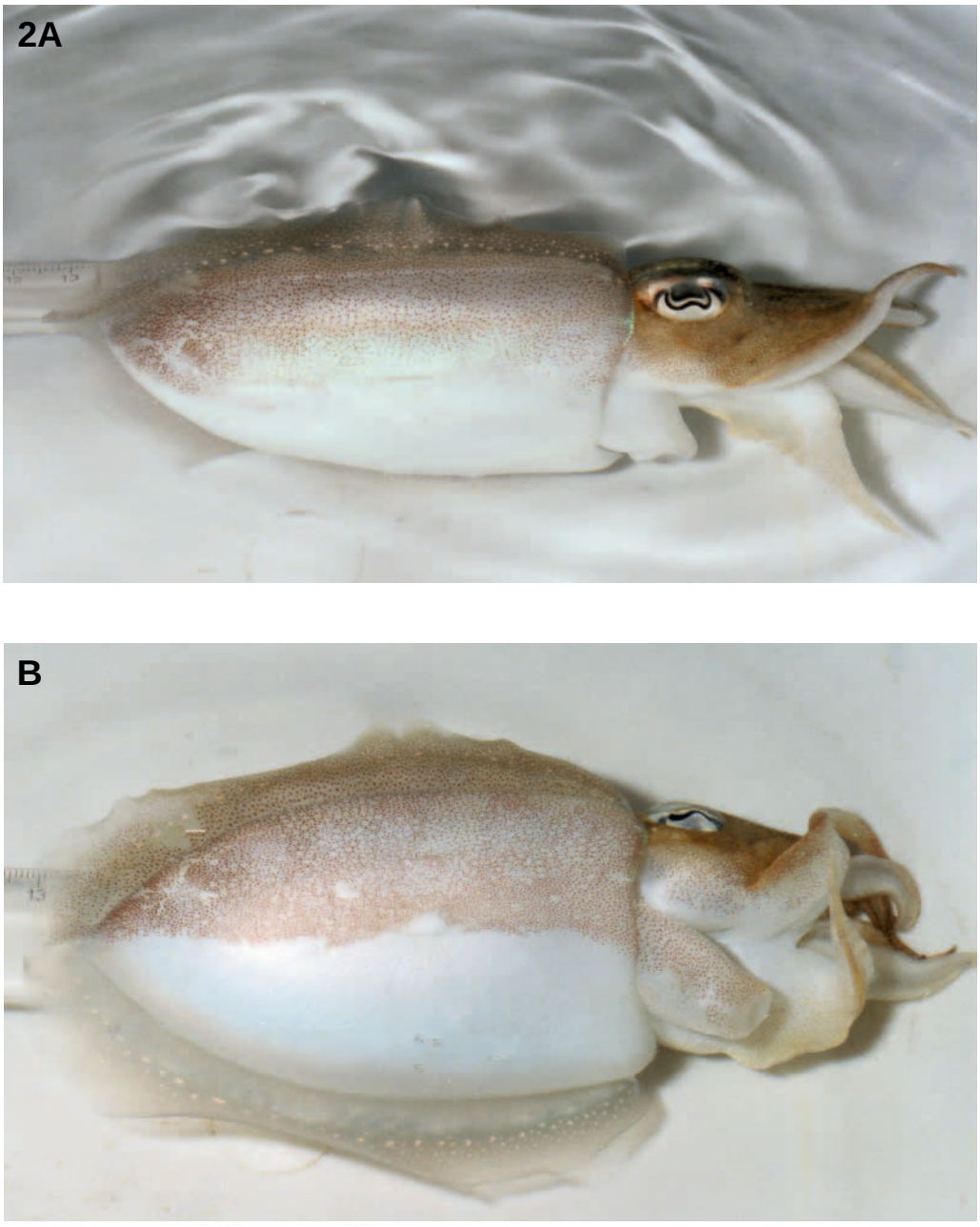

Fig. 2. The roll countershading reflex of *Sepia officinalis*. (A) Rotation through less than approximately 90˚ elicits component A: expanded chromatophores on the uppermost latero-ventral side of the animal. (B) Rotation through more than 90˚ adds component B, which extends to the midline of the animal. The slight irregularities in the otherwise sharp demarcation are due to skin lesions. Female, mantle length 100 mm.

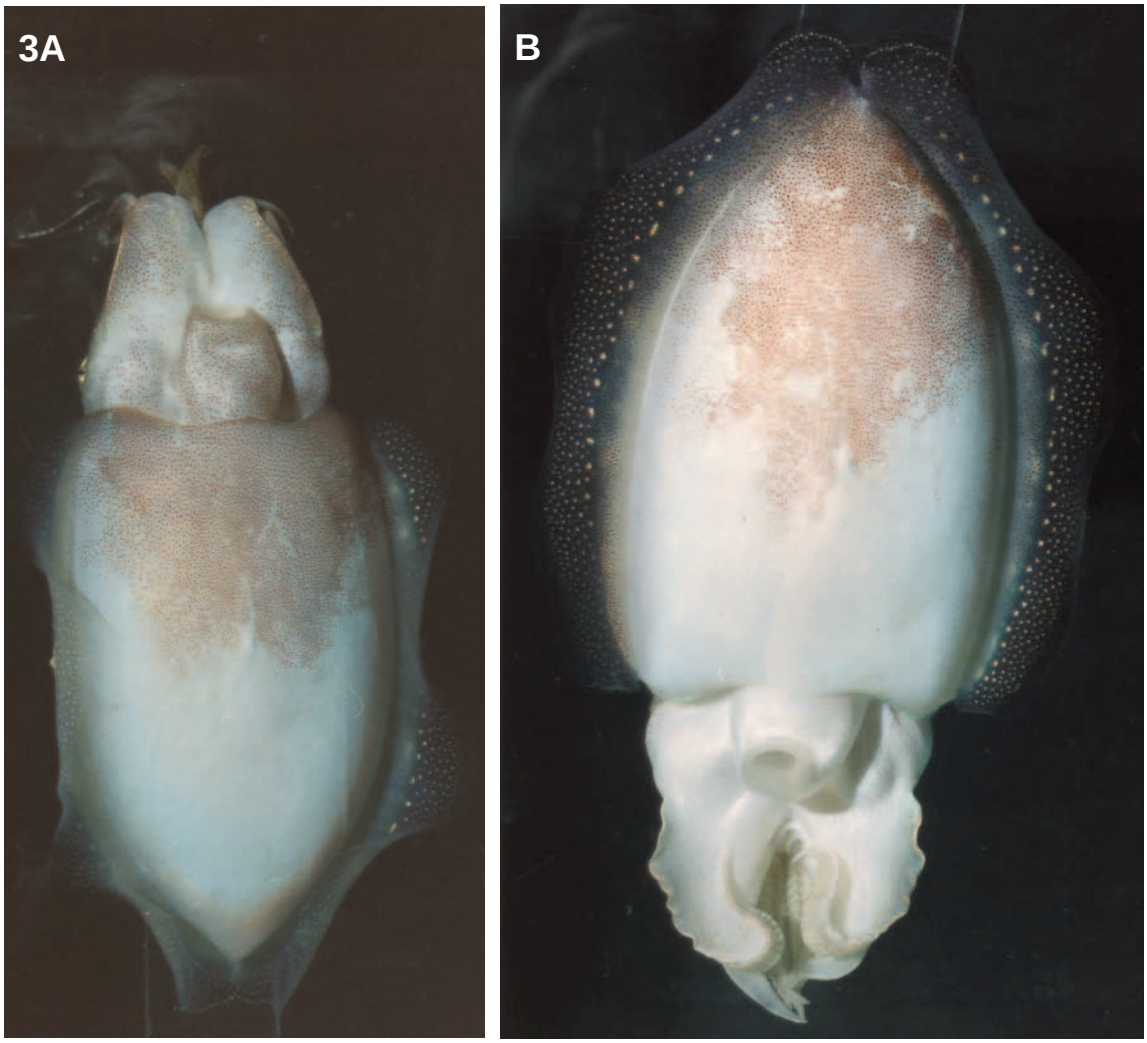

Fig. 3. The pitch countershading reflex of *Sepia officinalis*. (A) When the animal is head up, chromatophores on the anterior ventral surface of the body expand. (B) When the animal is head down, chromatophores on the posterior ventral surface expand. In both attitudes, the lower part of the body is paler than the upper part. Same animal as in Fig. 2.

'components' (Packard and Sanders, 1971). There are two components on each side of the body that are expressed differentially on the uppermost side during the CSR. The first response (component A) occurs when the rotation of the body is less than approximately 90° from the normal orientation of the animal. It consists of a broad longitudinal stripe of chromatophores that expand on the upper lateral edge of the ventral mantle and the ventral surface of the upper fin and on the part of the head that is posterior and ventral to the eye (Fig. 2A). Further rotation (from approximately 90° to approximately 180°) adds the second component (component B). This consists of chromatophores that expand on the upper half of the ventral mantle, funnel, head and arms. Component B extends as far as the midline of the animal, where it forms a sharply demarcated longitudinal border (Fig. 2B). The expansion of components A and B can last for at least 3 min.

The pitch countershading reflex

Rotating a cuttlefish in the pitch plane causes other chromatophore components to appear (Fig. 3). When the head is pointing up, chromatophores expand bilaterally over the ventral surface of the arms, head and funnel and on the anterior third of the mantle and fins (Fig. 3A). When the head points down, chromatophores expand bilaterally on the posterior two-thirds of the mantle and fins (Fig. 3B). The chromatophore components that expand during pitching have an irregular boundary across the mantle (unlike component B of the roll CSR, Fig. 2B). On the fins, only the chromatophores adjacent to the mantle expand. The pitch CSR can last for at least 3 min.

The countershading reflex during rotation around an axis oblique with respect to gravity

When a cuttlefish rolls whilst pitching, an 'intermediate' CSR is seen. Cuttlefish were first rotated 90° in the pitch plane into a head-up or head-down position: this elicits the pitch CSR. They were then inclined by about 30° and, in that inclined position, rotated in the roll plane. During such rotations, a modified pitch CSR is seen: it is no longer bilateral. Instead, the pitch CSR is now unilateral and chromatophores expand only on the body side that is uppermost during rotation.

Effects of statocyst operations on the countershading reflexes

The roll countershading reflex

Destruction of the gravity receptor systems. After bilateral destruction of all three gravity receptor systems, animals continue to show component A of the roll CSR on whichever side of the body is uppermost when the animal is rotated through approximately 90°; component B, however, no longer appears. After unilateral destruction of all three gravity receptor systems, animals show component A on whichever side of the body is uppermost (whether operated or unoperated), but component B no longer appears when the operated side is up. After unilateral removal of any one gravity receptor system (MSP, MNI or MNS), or any combination of two gravity receptor systems (MSP+MNS, MSP+MNI or MNS+MNI), both components of the roll CSR continue to be shown whichever side of the body is up (Table 1).

Table 1. *Effects of destroying gravity and angular acceleration receptor systems on the roll and pitch countershading reflexes (CSRs) of* Sepia

Sensory systems destroyed	Number of animals	Roll CSR				Pitch CSR	
		Component A		Component B			
		Intact	Operated	Intact	Operated	Intact	Operated
None (animal intact)	6	+	NA	+	NA	+	NA
Bilateral: all three gravity receptor systems	2	NA	+	NA	–	NA	–
Unilateral: all three gravity receptor systems	6	+	+	+	–	+	+
Unilateral: any one gravity receptor system	5	+	+	+	+	+	+
Unilateral: any two gravity receptor systems	3	+	+	+	+	+	+
Unilateral: all angular acceleration receptor systems	3	+	+	+	+	+	+

+ indicates the presence of the roll or pitch CSR; – indicates the absence of the roll or pitch CSR; NA, not applicable.

Destruction of the angular acceleration receptor systems. Unilateral destruction of the angular acceleration receptor systems has no effect on the roll CSR. Animals continue to show both components of the response, irrespective of whether the operated or the intact side of the body is up (Table 1).

The pitch countershading reflex

Destruction of the gravity receptor systems. Bilateral destruction of all three gravity receptor systems completely abolishes the pitch CSR; no chromatophore expansion occurs when animals are either in a head-up or a head-down position. In contrast, the pitch CSR persists after unilateral destruction of all three, any two or a single gravity receptor system (Table 1).

Destruction of the angular acceleration receptor systems. The pitch CSR is unaffected by unilateral destruction of the angular acceleration receptor systems. Animals continue to show the pitch CSR bilaterally when the head or the posterior end of the mantle is up (Table 1).

Effects of blinding on the countershading reflexes

To determine whether visual input is involved in the production of the CSRs, we examined bilaterally blinded animals, either with intact statocysts (N=2) or with all three gravity receptor systems destroyed unilaterally (N=1). Blinding alone has no effect on either the roll CSR or the pitch CSR. Blinding combined with unilateral destruction of all three gravity receptor systems has no effect on the pitch CSR. It does, however, affect the roll CSR; neither component A nor component B occurs, indicating that component A of the roll CSR is driven by input from the eyes as well as by input from the ipsilateral statocyst.

Brain pathways responsible for the countershading reflexes

Brain lesions were performed to determine whether the sensory input from the statocysts is transmitted to the chromatophore lobes through the suboesophageal brain or whether it runs through 'higher' centres in the supraoesophageal brain. Removal of the entire supraoesophageal brain (N=3) abolishes the roll CSR bilaterally, whereas unilateral removal of the supraoesophageal brain (N=4) abolishes the reflex only on the operated side (the pitch CSR was not investigated in these animals). These results show that the information from the statocysts is transmitted to the chromatophore motoneurones *via* the supraoesophageal brain.

The supraoesophageal brain areas that are most likely to be involved in controlling the CSRs are the left and right lateral basal lobes (see Discussion). If a lateral basal lobe is removed unilaterally (N=2), the operated side shows neither a roll nor a pitch CSR, but the intact side continues to give normal reflexes.

Discussion

The chromatic components of the countershading reflexes

The experiments described in this paper extend the previous work of Ferguson and Messenger (1991). They show that cuttlefish have a CSR that maintains their countershading when they are displaced in the pitch as well as in the roll plane.

Altogether there are six chromatic components of CSRs. The pitch CSR has an anterior and a posterior component, one expressed when the head is up, the other when the head is down. The roll CSR has a left and a right component A and a left and a right component B. All four of these are expressed when the animal is upside down. The two separate components of the roll CSR on each side of the body were not seen in the previous study of cephalopod countershading (Ferguson and Messenger, 1991), when the roll CSR was defined simply as an expansion of the ventral chromatophores as far as the midline of the animal (i.e. component B). There was some individual variation in the strength of the CSRs expressed in our experiments. This may be because we observed the animals under weak anaesthesia, the level of which we were unable to control precisely.

There is also an 'intermediate' CSR produced when an animal rolls as it pitches. Thus, irrespective of how their body is displaced, cuttlefish can maintain their countershading by selectively expanding different chromatophore components. Whether this is also true for *Loligo* and *Octopus*, both of which have a roll CSR (Ferguson and Messenger, 1991), remains to be investigated.

It is important to realise that cephalopod chromatophores can participate in different chromatic components (Maynard, 1967; Packard, 1982). Many of the chromatophores used in the pitch CSR are also used in the roll CSR; for example, those on the posterior part of the mantle (compare Figs 2 and 3). Moreover, chromatophores involved in the CSRs are almost certainly utilised in the chromatophore components shown when a cuttlefish is orientated normally; for example, some of the chromatophores that contribute to component A of the roll CSR are also expanded when an animal shows the 'latero-ventral patches' described by Hanlon and Messenger (1988). Although the iridophores may make some contribution to countershading in normally orientated animals, they are

not involved in the countershading *reflexes*. It is true that the structural colours produced by squid iridophores can change under the influence of acetylcholine (Hanlon *et al*. 1990; Cooper *et al*. 1990), but the time course of such changes (minutes, rather than seconds) clearly rules out any involvement in the responses reported here.

Sensory control of the countershading reflexes

The present experiments demonstrate that gravity receptor systems elicit the CSRs; angular acceleration receptor systems are not involved. This is not surprising, as angular acceleration receptor systems do not, in general, provide information about the direction of the gravito-inertial force. Also, the CSRs can persist for at least 3 min, and only gravity receptor systems could provide the long-lasting positional information necessary for maintaining such a response. The duration of the CSRs seen during the present experiments was considerably longer than that reported previously (Ferguson and Messenger, 1991), perhaps because in the earlier study fewer animals were tested.

A full ipsilateral roll CSR occurs even when only one of the three gravity receptor systems is left intact. There is no evidence of any additive effect of the gravity receptor systems, such as occurs in the control of compensatory head and eye movements in *Sepia*, where a progressive reduction in the amplitude of the response is seen as the number of intact gravity receptor systems is reduced (Budelmann, 1975).

An unexpected finding of the present experiments is that light is involved in eliciting countershading. However, this is only true for component A of the roll CSR. When the eyes are covered, this component is no longer shown on the side on which the gravity receptor systems are destroyed. It is not obvious why light affects only component A of the roll CSR. The lateral part of the ventral mantle is, however, the most visible part when a cuttlefish rolls. This, together with the fact that small displacements in the roll plane must occur more frequently than large ones, suggests that there may be an adaptive advantage in having this component under dual control. Further experiments are needed to establish the nature of the visual cues involved in eliciting component A. The present experiments show, however, that light almost certainly influences the roll CSR *via* the eyes rather than *via* the extraocular photoreceptors (Mauro, 1977).

Brain pathways involved in the countershading reflexes

As predicted by Ferguson and Messenger (1991), the present experiments show that the lateral basal lobes are part of the neuronal circuitry that produces cephalopod CSRs. The lateral basal lobes are known to be ‘higher’ brain centres involved in the production of chromatophore activity. Electrical stimulation of these lobes causes expansion of chromatophores, including those on the ventral surface (Boycott, 1961). Their efferent fibres project to the anterior and posterior chromatophore lobes (Boycott, 1953; Young, 1976, 1977; Novicki *et al*. 1990). They receive input from the eyes (Young, 1977; Messenger, 1979; Novicki *et al*. 1990) and probably from the statocysts (Young, 1977). In contrast, there are no known connections between the statocysts and the chromatophore lobes.

The present experiments suggest that each statocyst projects to the chromatophore

lobes *via* the ipsi- and the contralateral lateral basal lobes, for the pitch CSR continues to be expressed bilaterally after unilateral destruction of the gravity receptor systems.

Biological significance of the countershading reflexes

In a commentary on the previous paper on the roll CSR of cephalopods (Ferguson and Messenger, 1991), Greenwood (1991) questioned whether the reflex was used to avoid detection by predators or by prey. The major role of the CSR in the roll plane is almost certainly that of camouflage from predators. Because of the stability provided by the gas-filled cuttlebone, it is only under unusual circumstances that *Sepia* become disorientated in the roll plane, and at such times they are probably fleeing rather than attacking. In contrast, the countershading produced in response to rotation in the pitch plane is likely to help avoid detection by both predators and prey, since *Sepia* often swims up or down through the water column to attack prey (Messenger, 1968).

We thank Drs A. De Santis, S. Schrieber, S. Haas and C. Picco for help with behavioural testing; Drs A. Di Cosmo and G. Avagliano for preparing brain sections; Dr J. G. Boal for comments on a previous draft of the manuscript; and the President, Director and staff of the Stazione Zoologica for support and the use of facilities. B.U.B. acknowledges travel support from the Marine Medicine Budget of The Marine Biomedical Institute, The University of Texas Medical Branch at Galveston.

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