

Ludovic Dickel
Marie-Paule Chichery
Raymond Chichery

Laboratoire de Psychophysiology
Université de Caen
14032 Caen Cedex, France
and Centre Régional
d'Etudes Côtières,
14530 Luc-sur-Mer, France

Increase of Learning Abilities and Maturation of the Vertical Lobe Complex During Postembryonic Development in the Cuttlefish, *Sepia*

Received 24 July 2000; accepted 28 February 2001

ABSTRACT: When shown prawns in a glass tube, cuttlefish quickly learn to inhibit their predatory behavior. By using a visual learning paradigm, we studied training and retention performances of cuttlefish aged from 8 to 90 days. We found an improvement in the acquisition of learning abilities during the first 2 months of life as well as an increase of 24-hr retention performance between 30 and 90 days of age. Using morphometric measurements of different lobes of the central nervous system, we correlated the emergence of these learning abilities with the postembryonic development of related nervous structures. Our results show that only the growth of the superior frontal and vertical lobes appears to be significantly correlated with the improvement of learning and long-term retention performances. Thus, as found in earlier data collected in *Octopus*, the vertical lobe complex of the cuttlefish seems to be involved in these learning processes. © 2001 John Wiley & Sons, Inc. *Dev Psychobiol* 40: 92–98, 2001

Keywords: cephalopod; cuttlefish; development; learning; memory; vertical lobe complex

Cephalopods have adopted, during evolution, different predatory strategies that allow them to compete with vertebrates such as fishes. Among invertebrates, cephalopods present several advantages in the study of mechanisms underlying learning and memory. The brain is constituted by 37 (octopods) or 38 lobes (decapods) arranged around the esophagus. It is subdivided in supra-, peri-, and subesophageal masses which are laterally connected to two large optic lobes. Each lobe is constituted by a central fiber area (the neuropil) and a surrounding cortex (body cells). In

fact, this central nervous system, by far the most highly evolved of the mollusks, gives them unexpected learning abilities such as tactile or visual discrimination. This evolutionary background provides some interesting opportunities for comparative analyses.

Sepia officinalis is an active predator able to catch shrimps, fishes, and crabs of a size that is large relative to its own. There are two methods of attacking a prey: An attack involves either the ejection of the prehensile tentacles to seize a prey or the use of all the arms once the animal has pounced upon its prey (Duval, Chichery, & Chichery, 1984; Messenger, 1968). Fast-moving prey (such as fishes and shrimps) are preferentially attacked by the rapid shooting out of the two tentacles (occurring in less than 15 ms at 25°C); this final event constitutes the “strike” (Messenger, 1968).

Correspondence to: L. Dickel

A novel contextual situation, where shrimps placed inside a transparent tube are presented to a cuttlefish, led to a learned suppression of tentacle strikes (Messenger, 1973a). Such an experimental situation induces *Sepia officinalis* to reduce the number of strikes in the course of eight presentations (3 min each) of shrimps enclosed in a glass tube. This waning of capture attempts has a memory trace since cuttlefish still show few tentacle strikes during a retention test carried out 24 hr after the initial training. Such a stimulus-specific waning of the tentacle strikes has been considered as due to the lack of positive reinforcement or to the presence of negative reinforcement (The impacts of the tentacle clubs on the glass of the tube at each strike may be painful, as suggested by Messenger [1977]) Because an experimental modification of the amount of negative reinforcement received at each attempted capture affects the waning of the attack response, this learning has been recognized as a form of associative learning (Messenger, 1973a, 1977).

The brain structures mentioned next are visible in sagittal sections of the supraesophageal mass (Figure 1) in newly hatched and in adult cuttlefish.

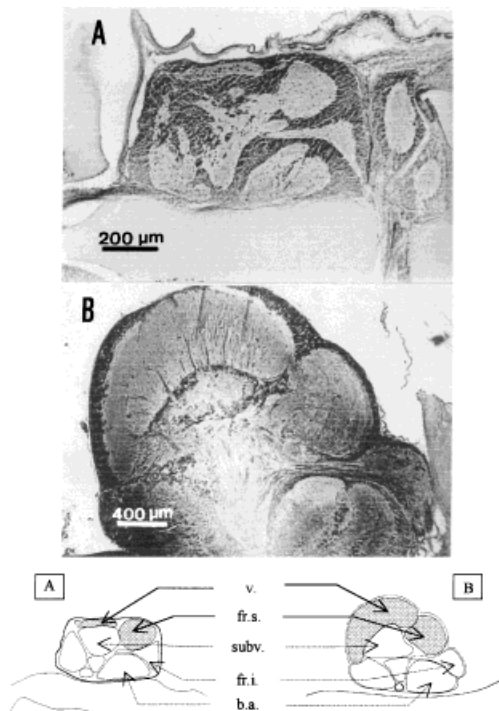


FIGURE 1 Sagittal section near the midline through the supraesophageal mass of a brain of a newly hatched (A) and an adult (B) cuttlefish. Notice the relative growth of the vertical lobe. b.a. = anterior basal lobe, fr.i. = inferior frontal lobe, fr.s. = superior frontal lobe, subv. = subvertical lobe, v. = vertical lobe.

Sanders and Young (1940) showed that removal of the vertical lobe impairs visual learning performance in cuttlefish. Furthermore, numerous studies in *Octopus* emphasized the role of the vertical lobe complex (vertical and superior frontal lobes) in the visual learning processes (for review, see Sanders, 1975).

The memory ability is poor in young *Sepia* (Dickel, Chichery, & Chichery, 1998; Wells, 1962) and is mainly related to the immaturity of the vertical lobe (Messenger, 1973b, Figure 1). Dickel, Chichery, and Chichery (1997) confirmed this evidence by studying short-term memory processes involved in the predatory behavior of *Sepia officinalis* from hatching to 9 days of age. In the same framework, the aim of this study was to determine if there is a correlation between improvement of learning and retention abilities and the growth of superior frontal and vertical lobes during development in *Sepia*. With prey-catching abilities being strongly implicated in this learning paradigm, the relative developments of two other structures also were followed: inferior frontal and anterior basal lobes, which are involved in motor programs associated with the predatory behavior (Chichery & Chichery, 1987, 1991).

This study provides evidence of a relationship between the growth of the vertical lobe complex and the improvement of short- and long-term memory storage in *Sepia officinalis* during the development of juveniles from 8 days to 3 months of age.

MATERIAL AND METHODS

Animals

Individuals of *Sepia officinalis* used in this experiment came from one egg batch that was maintained in the laboratory over a period of 31 days until hatching occurred (under controlled conditions, water temperature = $20.5 \pm 1^\circ\text{C}$). The dorsal mantle length (DML) of newly hatched animals was 7.4 ± 0.6 mm. Cuttlefish were kept for the first 30 days of life individually isolated in opaque plastic tanks ($120 \times 90 \times 35$ mm) with well-oxygenated sea water that was sterilized by UV light. From 30 days on, animals were maintained in larger tanks ($210 \times 90 \times 35$ mm). They were fed daily for the first 10 days with mysis and fry fish and thereafter with live shrimps of suitable size (*Crangon crangon*). Animals were tested at 8, 15, 30, 60, and 90 days posthatch (average DML of 10.4 ± 0.6 mm, 11.5 ± 0.5 mm, 18.1 ± 0.7 mm, 30.3 ± 1.2 mm, and 43.9 ± 2.7 mm, respectively).

Procedures

The experimental procedure used is similar to that already set up for adults (Chichery & Chichery, 1992a, 1992b; Messenger, 1973a) and juveniles of *Sepia officinalis* (Messenger, 1973b). Briefly, several individuals of common prey (mysis and crangonid shrimps for 8- to 15-day-old animals, shrimps only for 30- to 90-day-old animals) were enclosed in a glass tube. Its size was adapted to that of the young cuttlefish (15 mm diameter for 8- to 15-day-old animals, 30 mm diameter for 30- to 90-day-old ones). Cuttlefish usually attack moving prey (Duval et al., 1984; Messenger, 1968). Therefore, to optimize the attractiveness of the prey enclosed in the glass tube, shrimps or mysids were kept constantly moving in the tube by a current of water (Chichery & Chichery, 1992a).

To ascertain a high level of feeding motivation prior to behavioral testing, a shrimp hanging from a thread was presented to the cuttlefish. If this prey was attacked, it was removed before it could be seized. Only cuttlefish that promptly attacked (within about 10 s) were used for subsequent experiments. Before the experimental trials, animals were starved for 24 hr. In each experimental tank, the glass tube containing prey hidden behind an opaque plastic cylinder carefully placed around the glass tube was introduced at least 12 hr prior to the start of the learning session. In all learning and retention sessions, the apparatus was always in the same location in the tank.

The experiment began in the morning by removing the opaque cover, allowing the cuttlefish to visually detect the prey enclosed in the glass tube. For each animal, eight training sessions (3 min each) were carried out at 30-min intervals. At the end of each session, the opaque cover was refitted onto the glass tube. Retention tests were performed after 24 hr, during which time the cuttlefish were not fed. During each training session and during the retention test, the number of strikes against the glass tube was recorded minute by minute. The cuttlefish was given a shrimp at the end of each experiment in order to evaluate the interest of the cuttlefish in free-swimming prey despite the training and the retention test. All animals were tested only once.

Neurohistological Analysis

Some cuttlefish were sacrificed after retention tests (9 cuttlefish at 8 days of age, 5 cuttlefish each at 15, 30, 60, and 90 days). The specimens were fixed and preserved for several months in neutralized 10%

(wt/vol) formalin in sea water. The younger specimens were fixed in their entirety while those from 30 to 90 days old were decapitated, and the eyes were removed to facilitate fixation.

The fixed animals were Cajal silver stained (Young, 1971). After double inclusion (celloidin-paraffin) serial cross sections, 10 μ m thick, were made using a horizontal microtome.

The volume of the brain structures was measured by computer-image analysis based on the outlines of the whole supraesophageal mass of the brain containing the integrative and superior motor lobes (Boycott, 1961). In the measurement of the supraesophageal mass, we excluded all structures situated below a horizontal limit lying just above the esophagus (e.g., the lateral basal lobes), the ventral limit of which being broadly continuous with the magnocellular lobe (Young, 1977). The vertical, superior frontal, inferior frontal, and anterior basal lobes were drawn on the serial cross sections (intersection window = 50 μ m). These volumes were complemented with the remaining portions of the structures present on the one, two, three, or four sections which were not taken into account in the previous window. The anterior and posterior limits of the supraesophageal mass of the vertical and superior frontal lobes were selected on the basis of easily recognizable anatomical criteria (Dickel et al., 1997). The anterior and posterior limits of the anterior basal lobe were defined as the appearance of the neuropil of the anterior anterior basal lobe and the disappearance of the neuropil of the posterior anterior basal lobe, respectively. To use the same ventral limit as with the supraesophageal mass, we did not take into account the most lateroventral part of the posterior end of the anterior basal lobe. Identification of the anterior limit of the inferior frontal lobe was easily achieved by observing the appearance of the neuropil; the posterior limit was set when the neuropil started to divide into the two cerebral tracts. As the anterior and posterior limits of the cortices of the structures mentioned earlier were difficult to accurately determine, we excluded the sections containing only cortex (i.e., anteriorly and posteriorly to the neuropil) for each lobe.

Data Analysis

To evaluate the training performances within each age group, the numbers of strikes exhibited by the cuttlefish during Session 8 of the training were compared with those observed during the initial training session (using Wilcoxon paired-sample test). To compare training and retention performances between age groups, whatever the initial number of tentacle strikes,

the numbers of attempted captures during Session 8 of training and the 24-hr retention test were expressed as percentages of the response recorded during the initial training session. Age effects on training and retention performances were determined using Kruskal-Wallis one-way ANOVA. The correlation between the improvement in learning performance and the relative growth of the brain structures considered in this study were determined using the Pearson coefficient of correlation.

RESULTS

Initial Number of Strikes

The mean number of tentacle strikes at the beginning of each training session ranged from 17.9 ± 1.32 (15-day-old cuttlefish) to 13 ± 1.19 (90-day-old cuttlefish). However, Kruskal-Wallis one-way ANOVA analysis indicated that age had no significant effect on the number of tentacle strikes during the first 3-min presentation of the learning apparatus ($H = 5.3$, $df = 4$).

Training Performance

Figure 2 shows a gradual improvement in training performances in the course of post-embryonic development. The waning in the number of strikes in the course of the 8 training sessions is only significant for the 15-day-old ($n = 10$, $Z = -2.7$, $p < .01$), 30-day-

old ($n = 10$, $Z = -2.5$, $p < .05$), 60-day-old ($n = 11$, $Z = -2.9$, $p < .01$) and 90-day-old ($n = 11$, $Z = -2.9$, $p < .01$) cuttlefish.

Age had a significant effect on training performance ($H = 25.2$, $df = 4$, $p < .01$). The rate of strikes observed during training Session 8 ranged between $91.2 \pm 6.1\%$ at 8 days to $12.1 \pm 4.2\%$ at 90 days (Figure 2). However, Figure 3 shows a significant time effect on the number of strikes displayed by 8-day-old cuttlefish within sessions (all sessions pooled, ANOVA, $F(2, 267) = 31$, $p < .001$). In fact the number of attempted captures decreases between the first and the third minute of the training within sessions (all sessions pooled for the 10 subjects, Student t test for paired data, $N = 90$, $T = 6.6$, $p < .001$).

Retention Performance

The number of strikes during the retention test differs from those of the 3-min duration of the initial session only at 30 days ($n = 10$, $Z = -2.1$, $p < .05$), at 60 days ($n = 11$, $Z = -2.4$, $p < .05$), and at 90 days ($n = 11$, $Z = -2.9$, $p < .01$) of age.

Figure 2 shows a gradual improvement in 24-hr retention performance during development. The rate of strikes observed during the retention test waned from $106.7 \pm 16.1\%$ at 8 days to $27.31 \pm 8.3\%$ at 90 days. Here again, a Kruskal-Wallis one-way ANOVA showed a strong group effect, $H = 22.7$, $df = 4$, $p < .001$. After the retention test, all animals promptly attacked a free-swimming prey placed near the learning apparatus.

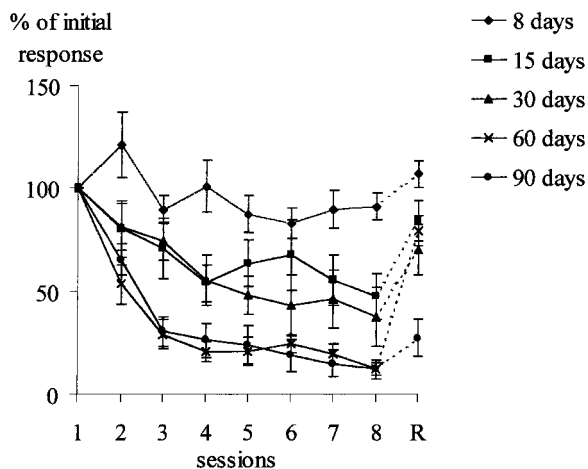


FIGURE 2 Learning curves of cuttlefish at 8 days ($n = 10$), at 15 days ($n = 10$), at 30 days ($n = 10$), at 60 days ($n = 11$), and at 90 days ($n = 11$) of age. R = 24-hr retention test. The vertical bars indicate SEM.

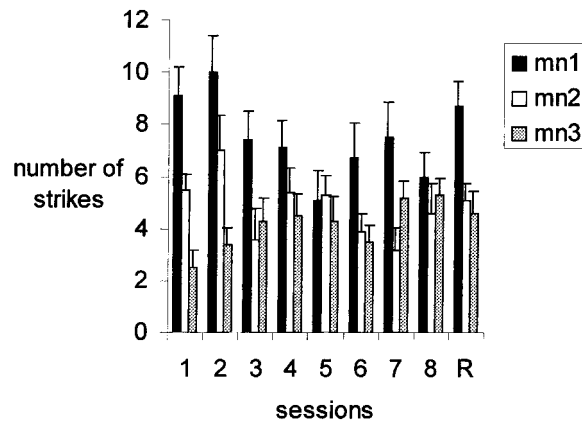


FIGURE 3 Number of strikes recorded each minute plotted for learning and retention sessions in 8-day-old animals. R = 24-hr retention test, mn = minute. The vertical bars indicate SEM.

Neurohistological Analysis

The vertical and superior frontal lobes developed more rapidly than the supraesophageal mass during the first 3 months of postembryonic life (significant age effect on relative growth, $H = 26.6$, $df = 4$, $p < .01$ and $H = 25.5$, $df = 4$, $p < .01$, for vertical and superior frontal lobes, respectively). On the other hand, the anterior basal lobe grew more slowly than the supraesophageal mass (significant age effect, $H = 22.5$, $df = 4$, $p < .01$). The inferior frontal lobe appeared to grow nearly isometrically with the supraesophageal mass ($H = 2.6$, $df = 4$, Figure 4).

Correlation Between Neurohistological and Behavioral Data

The data (Table 1) suggest that during the first 3 months of postembryonic life, the relative growth of the inferior frontal and anterior basal lobes are not correlated either with the improvement of acquisition or retention performances during development (A positive coefficient of correlation means that the relative volume of the structure decreases when learning performance increases.) In the same way, improvement of the acquisition and the 24-hr retention performances are clearly related to the growth of the superior frontal and vertical lobes.

DISCUSSION

Learning Performance During Development

The experiments reported in this article demonstrate that cuttlefish have different memory traces of a

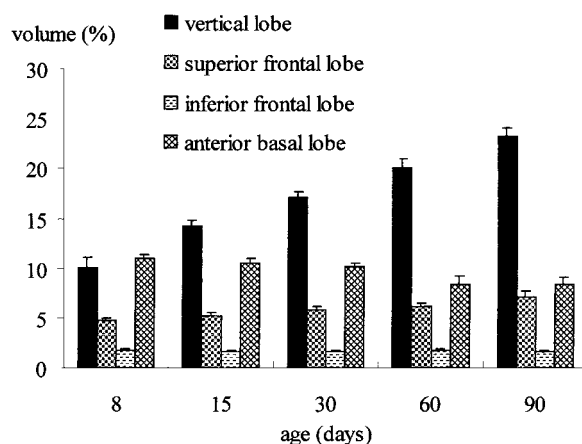


FIGURE 4 Relative volume of the vertical, superior frontal, inferior frontal, and anterior basal lobes during development. All the volumes are expressed as a percentage of the total volume of the supraesophageal mass. The vertical bars indicate SEM.

negative feeding experience depending on their age. Although 8-day-old *Sepia officinalis* possess a complete feeding motor pattern that is indistinguishable from that of adult animals (Boletzky, 1987; Dickel et al., 1997; Wells, 1958), the level of waning of tentacle strikes made against the glass tube is significantly different from that exhibited by animals of other ages. Messenger has demonstrated that this behavioral decrement is not the result of motor fatigue or a temporary incapacity to make a tentacle ejection (Messenger, 1973a). In this study, all animals were juveniles, and experiments were carried out in the summer during a phase of rapid growth. There is no significant age effect on number of tentacle strikes during the first training presentation, and all tested cuttlefish promptly caught a free shrimp in the tank at the end of each retention test. Thus, in cuttlefish, the improvement of performance observed from 8 to 90 days of age in training and retention is specifically related to the juvenile's learning capacities, not to any change in feeding motivation during development.

Analysis of learning performance during development (Figure 2) confirmed earlier results (Dickel, Boal, & Budelmann, 2000; Dickel et al., 1998; Messenger, 1973b). At 8 days of age, with a training of eight successive trials (separated by 30 min), the short-term memory capacities required for obtaining a good training performance were deficient. During this training, 8-day-old animals displayed significant acquisition of the task within learning sessions (Figure 3), confirming the existence of some short-term memory abilities at this age (Dickel et al., 1997). However, the interval in time between sessions (30 min) was longer than was the animals' short-term memory span as determined in adult animals (Messenger, 1971).

At 30, 60, and 90 days, animals showed significant learning acquisition, with the number of strikes during the training Session 8 being lower than those occurring during the initial session (Figure 2). At these ages, the short-term memory is still developing, with storage of information getting up to 30 min, which confirms previous data (Dickel et al., 1998).

A significant improvement of the performance during the 24-hr retention test also was recorded from 30 to 90 days. These results would seem to confirm the gradual increase in the duration of long-term retention during postembryonic development.

Setting Up of Memory Processes and Development of the Vertical and Superior Frontal Lobes

Considering the limits of correlational studies, the anterior basal lobe involved in motor programs

Table 1. Correlation Between Behavioral and Histological Data

	Relative Growth of the Vertical Lobe	Relative Growth of the Superior Frontal Lobe	Relative Growth of the Inferior Frontal Lobe	Relative Growth of the Basal Anterior Lobe
Training Performance	−0.955 ^{a,b}	−0.899 ^{a,b}	0.446	0.897
24-hr Retention Performance	−0.895 ^{a,b}	−0.945 ^{a,b}	0.817	0.725

^aPositive relation between relative growth of the CNS structures and increase of training or retention performance.

^bSignificant correlation.

associated with the predatory behavior (Chichery & Chichery, 1987) appeared not to be positively related with the improvement of learning capacities during development (training and 24-hr retention performances). Moreover, our analysis showed that the relative growth of the inferior frontal lobe (involved in motor programs associated with paralysis of the prey; Chichery & Chichery, 1991) was not significantly correlated with the changes of learning and retention capacities of cuttlefish during the first 3 months of life (Table 1). Since the relative volume is expressed as a percentage of the whole supraesophageal mass (including the vertical lobe complex), a decrease in relative volume of these structures means that their growth appears insignificant compared to that of the vertical and superior frontal lobes. It may confirm that these behavioral changes cannot be due to a major maturation of motor abilities.

The strong correlation between the relative growth of the vertical and superior frontal lobes and the improvement of acquisition and long-term retention performances during postembryonic development appears in agreement with previous data. In fact, experimental brain lesions on the octopus have provided some partial answers about the influence of each of these lobes in the acquisition and retention processes. The vertical lobe seems to be involved in acquisition during training (Boycott & Young, 1955; Maldonado, 1963; Young, 1965) as well as in retention processes (Young, 1961, 1965). The vertical lobe contains numerous microneurons (the extensions of which remain restricted to the neuropil of the vertical lobe; Young, 1971, 1979). Young (1960) underlines the likely role played by these cells in data processing, particularly in “building-up” associations among various stimuli in the course of associative learning. In cuttlefish, learning performance improves gradually, being linked to the growth of the vertical lobe during development; similarly, lesions of the vertical lobe in the adult *Octopus* (Young, 1958) have shown that the memory deficit was closely linked to the size

of the lesion. However, it remains important to determine what cell types are involved and whether the increased volume of these lobes is due to cell multiplication and/or substantial neuritic growth (Previous studies showed an increase in the number of nerve cells in the octopus during postembryonic development; Packard & Albergoni, 1970.)

Based on lesion experiments on the superior frontal lobe in *Octopus*, several authors have mentioned the involvement of this structure in learning processes (Maldonado, 1965; Nixon & Young, 1966; Young, 1964). In cuttlefish, the superior frontal lobe receives sensory inputs directly from the arms (Budelmann & Young, 1987). In *Sepia*, this lobe may act as an “amplifier” of nociceptive inputs from the tentacle clubs during the acquisition of learned suppression of tentacle striking. This would explain the correlation that we found between postembryonic relative development of this lobe and improved training performance (Table 1). In this way, taking into account the tentacle strikes on the glass tube occurring during the retention test, the superior frontal lobe also could play an important role in keeping a low level of attempted capture 24 hr after the training session.

Many methodological difficulties have been reported in the study of the setting-up of memory processes in mammals, notably a difficulty in controlling the in utero environment of animals, sensorimotor immaturity in young mammals during the early postembryonic phase, and interference with the enrichment of individual experience during the retention phase (Campbell & Spear, 1972). In cuttlefish, it is easy to maintain strict control over conditions during embryonic development and growth of young cuttlefish (Dickel et al., 2000). Both their lifestyle and strategies of capturing prey remain identical throughout postembryonic development until adulthood (Boletzky, 1987; Wells, 1958). The cuttlefish thus appears to be an interesting model for the study of the complex phenomenon involved in the ontogeny of memory.

NOTES

We thank C. Marais for her technical assistance. We are particularly grateful to Dr. S. von Boletzky and S. Cobb for helping to correct the English translation.

REFERENCES

- Boletzky, S. von (1987). Juvenile behaviour. In P. R. Boyle (Ed.), *Cephalopod life cycles*. (Vol. II, pp. 45–84). London: Academic Press.
- Boycott, B. B. (1961). The functional organization of the brain of the cuttlefish, *Sepia officinalis*. *Proceedings of the Royal Society of London*, 153, 503–534.
- Boycott, B. B., & Young J. Z. (1955). A memory system in *Octopus vulgaris*. *Proceedings of the Royal Society of London*, 143, 449–480.
- Budelmann, B. U., & Young J. Z. (1987). Brain pathways of the brachial nerves of *Sepia* and *Loligo*. *Philosophical Transactions of the Royal Society of London*, 315, 345–352.
- Campbell, B. A., & Spear, N. E. (1972). Ontogeny of memory. *Psychological Review*, 79(3), 215–236.
- Chichery, M. P., & Chichery, R. (1987). The anterior basal lobe and control of prey-capture in the cuttlefish (*Sepia officinalis*). *Physiology & Behavior*, 40, 329–336.
- Chichery, M. P., & Chichery, R. (1991). The predatory behaviour of *Sepia officinalis*: Ethological and neurophysiological studies. In E. Boucaud-Camou (Ed.), *La seiche, the cuttlefish*. First International Symposium on the Cuttlefish *Sepia* (pp. 281–288). Caen, France: Centre de Publication de l'Université de Caen.
- Chichery, R., & Chichery, M. P. (1992a). Learning performances and aging in cuttlefish (*Sepia officinalis*). *Experimental Gerontology*, 27, 234–239.
- Chichery, M. P., & Chichery, R. (1992b). Behavioural and neurohistological changes in aging *Sepia*. *Brain Research*, 574, 77–84.
- Dickel, L., Boal, J. G., & Budelmann, B. U. (2000). The effect of early experience on learning and memory in cuttlefish. *Developmental Psychobiology*, 36(2), 101–110.
- Dickel, L., Chichery, M. P., & Chichery, R. (1997). Post-embryonic maturation of the vertical lobe complex and early development of predatory behavior in the cuttlefish (*Sepia officinalis*). *Neurobiology of Learning and Memory*, 67, 150–160.
- Dickel, L., Chichery, M. P., & Chichery, R. (1998). Time differences in the emergence of short- and long-term memory during postembryonic development in the cuttlefish, *Sepia*. *Behavioural Processes*, 44, 81–86.
- Duval, P., Chichery, M. P., & Chichery, R. (1984). Prey capture by the cuttlefish (*Sepia officinalis* L.): An experimental study of two strategies. *Behavioural Processes*, 9, 13–21.
- Maldonado, H. (1963). The general amplification function of the vertical lobe in *Octopus vulgaris*. *Zeitschrift für Vergleichende Physiologie*, 47, 215–229.
- Maldonado, H. (1965). The positive and negative learning process in *Octopus vulgaris* L.. Influence of the vertical and median superior frontal lobes. *Zeitschrift für Vergleichende Physiologie*, 51, 185–203.
- Messenger, J. B. (1968). The visual attack of the cuttlefish, *Sepia officinalis*. *Animal Behaviour*, 16, 342–357.
- Messenger, J. B. (1971). Two stage recovery of a response in *Sepia*. *Nature*, 232, 202–203.
- Messenger, J. B. (1973a). Learning in the cuttlefish, *Sepia*. *Animal Behaviour*, 21, 801–826.
- Messenger, J. B. (1973b). Learning performance and brain structure: A study in development. *Brain Research*, 58, 519–523.
- Messenger, J. B. (1977). Prey capture and learning in the cuttlefish, *Sepia*. *Symposia of the Zoological Society of London*, 38, 347–376.
- Nixon, M., & Young, J. Z. (1966). Levels of responsiveness to food or its absence and the vertical lobe circuit of *Octopus vulgaris*. *Zeitschrift für Vergleichende Physiologie*, 53, 165–184.
- Packard, A., & Albergoni, V. (1970). Relative growth, nucleic acid content, and cell numbers of the brain in *Octopus vulgaris*. *Journal of Experimental Biology*, 52, 539–552.
- Sanders, F. K. (1975). The cephalopods. In W. C. Corning, J. A. Dyal, & A. O. D. Willows (Eds.), *Invertebrate learning* (Vol. III, pp. 1–101). New York: Plenum Press.
- Sanders, G. D., & Young, J. Z. (1940). Learning and other functions of the higher nervous centres of *Sepia*. *Journal of Neurophysiology*, 3, 501–526.
- Wells, M. J. (1958). Factors affecting reactions to Mysis by newly hatched *Sepia*. *Behaviour*, 13, 96–111.
- Wells, M. J. (1962). Early learning in *Sepia*. *Symposia of the Zoological Society of London*, 8, 149–169.
- Young, J. Z. (1958). Effects of removal of various amounts of the vertical lobes on visual discrimination by *Octopus*. *Proceedings of the Royal Society of London*, 149, 441–462.
- Young, J. Z. (1960). Unit processes in the formation of representations in the memory of *Octopus*. *Proceedings of the Royal Society of London*, 153, 1–17.
- Young, J. Z. (1961). Learning and discrimination in the *Octopus*. *Biological Reviews*, 36, 32–96.
- Young, J. Z. (1964). Paired centres for the control of attack by *Octopus*. *Proceedings of the Royal Society of London*, 159, 568–588.
- Young, J. Z. (1965). The organization of a memory system. *Proceedings of the Royal Society of London*, 163, 285–320.
- Young, J. Z. (1971). *The anatomy of the nervous system of Octopus*. Oxford: Clarendon Press.
- Young, J. Z. (1977). The nervous system of *Loligo*: III. Higher motor centres. The basal supraoesophageal lobes. *Philosophical Transactions of the Royal Society of London*, B 276, 351–398.
- Young, J. Z. (1979). The nervous system of *Loligo*: V. The vertical lobe complex. *Philosophical Transactions of the Royal Society of London*, B, 285, 311–354.