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The cuttlefish *Sepia officinalis*
(N. Koueta, J.P. Andrade, S. v. Boletzky, eds)

BEHAVIOURAL AND NEURAL MATURATION IN THE CUTTLEFISH *SEPIA OFFICINALIS*

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DEVELOPMENT
BEHAVIOUR
LEARNING
CENTRAL NERVOUS SYSTEM
PREDATION
DEFENCE

ABSTRACT. – This paper briefly describes findings concerning the ontogenesis of behavioural and neural plasticity in cuttlefish. Predatory and defensive behaviours were investigated and learning and memory abilities were assessed during post-embryonic development. In parallel studies, the maturation of brain structures was determined at different ages. Learning abilities were poor and defensive strategies appeared relatively stereotyped in early juveniles. Memory developed and the plasticity of both defensive and predatory behaviour gradually increased during the first 3 months of life. These behavioural changes occurred simultaneously with the maturation of the most associative structures of the brain. Based on these laboratory observations, several hypotheses are proposed for the behaviour of juvenile cuttlefish in the field.

INTRODUCTION

In the last decades, the ontogenesis of behaviour in cephalopods has been the subject of relatively few detailed studies. These studies focused mainly on the predatory behaviour (Wells 1958, 1962, Boletzky 1983, 1987, Dickel 1997, Agin 2001) with some descriptions of certain defensive behaviours of the juvenile being mentioned in the literature (Boletzky 1987, Hanlon & Messenger 1988, Poirier 2004). Among cephalopods, juvenile cuttlefish are *apparently* miniature replicas of the adults. Like their parents, they assume a necto-benthic mode of life, feed on the same kind of prey and use the same prey-capture strategies: tentacle strikes for prey capable of a rapid escape (mysids, shrimp, fishes) or a "jump" strategy for less mobile prey such as crabs (Agin *et al.* 2006, Messenger 1968, Chichery & Chichery 1991). The juveniles also use the same way to conceal themselves in their environment (either changing colour or digging into the sand) or to escape potential predators (jet swimming and ink squirting). At hatching, the young do not benefit from any parental care. As a consequence they need to cope on their own with ecological demands: either to avoid or defend themselves against predators and to find, choose and capture available prey. For such an active and moving predator, these complex processes *a priori* require behavioural plasticity such as learning and memory capabilities. Therefore, even if motor and sensorial skills of juveniles seem to be equivalent to those observed in adults (Boletzky 1987, Dickel 1997, Poirier 2004), a question remains about the possible plasticity of predatory and defensive behaviour in juvenile cuttlefish.

Predatory behaviour

Feeding behaviour and post-embryonic yolk reserves

Juvenile cuttlefish are active predators (Boletzky 1987, Hanlon & Messenger 1996, Dickel 1997), able to catch and consume fast-moving prey such as young fishes, shrimps and mysids. Several authors have noticed that there is a period of few days before the first prey-capture by young cuttlefish, this period being interpreted as the time required for the newly-hatched animals to consume their yolk reserves (Wells 1958). However, juveniles start feeding prior to the total absorption of the inner yolk (Boletzky 1987). Furthermore, we have demonstrated that the volume of the inner yolk sac at hatching is greater in animals in which embryonic development was rapid due to high temperature. Concurrently, we have observed that hatchlings coming from eggs incubated at high temperature show a higher capture rate on the first day of postembryonic life than those coming from eggs incubated at a lower temperature. Thus, the amount of yolk available at hatching does not appear to determine the triggering of predatory behaviour of newly-hatched cuttlefish (Dickel *et al.* 1997).

Choice of prey

Most of our knowledge of prey selection has come from rearing experiments in laboratories (reviewed in Boletzky & Hanlon 1983) or from gut-contents analyses (Najai & Ktari 1979, Henry & Boucaud-Camou 1991, Blanc *et al.* 1998, Pinczon du Sel *et al.* 2000). Adult *S. officinalis* are considered to be generalist predators, feeding mainly on shrimp, crabs, and fishes. We recently showed that adult cuttlefish from the same fishing ground did not all display the same food preference, with some preferring shrimps and others preferring crabs (Darmaillacq *et al.* 2004a). Unfortunately, little is known about the diet of young animals, although this is of critical importance to better understand the cuttlefish's predatory behaviour.

Prey-preference in juveniles

Wells (1958) suggested that *S. officinalis* juveniles "innately" detect and recognize prey that have an elongate shape moving along their long axis (shrimp, mysids, young fishes). However, several authors have shown that juveniles are also able to feed on crabs (Henry & Boucaud-Camou 1991, Dickel 1997, Blanc *et al.* 1998). We were interested in determining whether juveniles had a preference for different types of prey during the first three months of life (Darmaillacq *et al.* 2004b). Previously unfed cuttlefish spontaneously preferred shrimp. This initial preference remains prevalent throughout the first month of life. These observations appear to concur with Wells' observations (1958) that juvenile cuttlefish more readily attack elongate moving prey as compared to crabs, which were always chosen less often. However, in a three way choice test conducted three days post-hatching where cuttlefish were offered a choice between crabs, shrimp and young fishes of suitable size at different ages, they preferred shrimp over fishes. This finding suggests that their visual prey recognition processes involve a high order visual identification rather than the basic characteristics (elongate shape moving along the long axis) used by toads and other animals (Ewert 1985, Prete 1999). After the first two months of life, the preference seems then to widen to include young fishes. This suggests that their diet range begins to diversify, regardless of their previous shrimp only diet.

Effect of feeding experience

We secondly examined whether it would be possible to change the shrimp preference of very young cuttlefish by restricting the first meal to crab, a usually non-preferred prey. Previously unfed 3-day-old juveniles of one group were fed a single crab and those of the other group were fed one shrimp. The animals of both groups were not fed until day 7. At this age, each animal was examined in a choice test between crabs and shrimp presented in a two-way apparatus. The results of the prey-preference experiment showed a significant preference for the original diet. In both groups, the majority of young *Sepia* selected the prey which they had first experienced (Darmaillacq *et al.* 2004b). At this point, a question remains unanswered: does a young cuttlefish "learn" to prefer a prey on the basis of its feeding experience (i.e. eating a prey being regarded as a reward) or are they able to choose a potential prey by simple visual familiarization, without food reinforcement?

Effect of early visual familiarization with a potential prey

We tested the effect on their subsequent prey choice by exposing a non-preferred prey (i.e. crabs) to *S. officinalis*, immediately after hatching and while still depending on their yolk reserves (Darmaillacq *et al.* 2006). With this aim, cuttlefish hatchlings were divided into three groups. In group 1, crabs were directly exposed to newly-hatched cuttlefish, for 5 h after hatching. Crabs were exposed to animals of group 2 for the same length of time but in this case young cuttlefish were enclosed in a glass cylinder (supplied with fresh sea water) so that they were not exposed to any chemical cues from the crabs. As a control, group 3 had no crab exposure. On day 3, all juveniles were given a two-way choice between crabs and shrimp. Overall, both groups of cuttlefish that had a crab exposure at hatching (groups 1 and 2) showed a preference for crabs over shrimp that was significantly different from the food preference of cuttlefish that had no previous crab experience. We found that a simple visual exposure of a naturally non preferred prey at hatching is sufficient to induce a significant change in the juvenile cuttlefish's initial preference. This induced preference suggests that the young cuttlefish can record the characteristics of the prey to which they were exposed only on the basis of visual cues, without any alimentary motivation, and to retain this information for at least three days. This may confer important adaptive advantages in the case of a changing environment. Actually, when they hatch, cuttlefish are at their most vulnerable stage. The embryonic food reserve available is relatively short-lived, so that choosing available prey items and consuming them rapidly after hatching is crucial for survival.

In the course of evolution, this behavioural trait was probably reinforced: if the kind of prey that cuttlefish are "genetically programmed" to capture is not available in the hatchlings' visual environment, juvenile cuttlefish that can shift their attraction toward other available prey will have an advantage over those that can not. Ultimately, the individual prey-preference observed in adults (Darmaillacq *et al.* 2004a) may depend on their early experience.

Prey hunting

Although cuttlefish are very active predators, Messenger (1973) noted the absence of pursuit of the prey in hatchlings. We have demonstrated that the post-embryonic maturation of prey-pursuit behaviour in hatchlings occurs earlier when their embryonic development is short (i.e. when the temperature of egg incubation is high, Dickel *et al.* 1997). The pursuit of a prey by a predator involves short-term memory, enabling remembering the prey when it moves out of the predator's frontal visual field (Sanders & Young 1940, Messenger 1973). Because of the involvement of the vertical lobe complex in visual memory processes in cephalopods (see Agin *et al.* in this issue), we examined the growth of the main lobes of the vertical lobe complex in early juveniles hatched from eggs incubated at different temperatures. We also followed the post-embryonic appearance of the vertical/subvertical lobe fibre tracts in the same animals. These tracts represent the main output fibers of the vertical lobe together with some afferent fibres from the subvertical lobe. The relative growths of the vertical and superior frontal lobes are not correlated with the maturation of the prey-pursuit behaviour. By contrast, the vertical/subvertical lobe tract appearance is highly correlated with the emergence of pursuit in juveniles, whatever the length of their embryonic development. It must be emphasized that pursuit deficits were also observed in senescent animals. In the latter, numerous degenerating fibres were found in the vertical/subvertical lobe tracts (Chichery & Chichery 1992).

Performance in learning not to attack a prey

Since *S. officinalis* hatchlings show the same basic behaviours as adults, a single learning paradigm is applicable at different stages of postembryonic development. Messenger (1977) devised a simple learning protocol to test learning and retention abilities in cuttlefish (see previous article Agin *et al.* 2006). During training, cuttlefish were offered shrimp enclosed in a glass tube. Cuttlefish normally capture mobile prey by rapidly shooting out their two long tentacles. In the experimental apparatus, the cuttlefish were unable to capture the prey and, instead, hit the glass tube. During massed training, or spaced training, cuttlefish showed a substantial waning of capture attempts. This learning has been recognized as a form of associative learning (Messenger 1977, Agin *et al.* 2006). With this paradigm, we showed a gradual improvement in both training and long-term retention performance in the course of the first three months of life. Moreover, we found a significant correlation between the improvement of learning and retention abilities and the growth of the superior frontal and vertical lobes during development (Dickel *et al.* 2001). In contrast, no correlation was found between retention abilities of juveniles and the relative volume of some of the brain structures that are involved in motor programs associated with the predatory behaviour (Chichery & Chichery 1987, 1991).

In early juveniles, the establishment of prey preference and the learning "not to attack a prey" are probably separate processes and, consequently, may depend on different neuronal substrates. In the first case, they learn fast and retain for a long time. In the second one, the learning requires several trials and the long-term retention is poor. Just like the vertical lobe complex, the optic lobes were supposed to play a role in visual memory processes, at least in *Octopus vulgaris* (reviewed in Sanders 1975). These lobes are particularly well developed in newly-hatched cuttlefish (Dickel 1997, Poirier 2004). We therefore can suggest that they would be involved in the establishment of prey preference in juveniles. Extensive work should be archieved to assess the validity of this hypothesis. Another hypothesis could be the following: behavioural inhibitions are generally more difficult to acquire by early juveniles than by adults, as observed in several species of vertebrate species, including rodents (reviewed in Myslivecek 1997). This phenomenon is generally linked to the development of the hippocampus in newborns (among others, the hippocampus is known to have an inhibitory role in the general level of activity, Bast & Feldon 2003). The vertical lobe complex could also be an inhibitory brain structure (as originally hypothesized by Sanders 1975). Thus, in juvenile cuttlefish (which have a poorly developed vertical lobe complex), it would be more difficult to learn to inhibit than to re-orientate predatory behaviour.

Defensive behaviour

The development of defensive behaviour has been the subject of very few studies in *S. officinalis* (Hanlon & Messenger 1988). As to the cryptic behaviour reported (Hanlon & Messenger 1996), cuttlefish can bury into sand to conceal themselves from potential predators. They can also quickly change colour, using their neurally controlled chromatophores to conceal themselves in their environment (reviewed in Messenger 2001).

Development of sand-digging

In *Sepia*, digging is a relatively complex, but short and apparently fixed behavioural sequence (lasting less than 5 s, Mather 1986). In our experiments, juvenile cuttlefish were observed daily in their rearing tanks, the bottom of which was covered with fine sand (Poirier *et al.* 2004). We observed very few and only partially buried cuttlefish some hours after hatching (less that 9% of them). Thereafter, the number of buried cuttlefish progressively increased to reach 85% at day 15. This gradual emergence of sand digging behaviour can be due to maturation of some behavioural abilities and/or developmental changes in their defensive strategy.

Development of body patterning

Chromatic components together with textural, postural and locomotor components, contribute considerably to body patterning (Packard & Sanders 1971, Hanlon & Messenger 1988). According to Packard & Sanders (1971), body patterns may be acute (shown for seconds or minutes) or chronic. Cuttlefish use chronic body pattern to conceal themselves (Hanlon & Messenger 1996). When the substrate is variegated or dark, cuttlefish achieve a disruptive pattern which "breaks" the natural outline of the body (Hanlon & Messenger 1988). When the substrate is uniform, cuttlefish show a general background resemblance adopting a similar brightness to the substrate (Hanlon & Messenger 1988). These authors observed that when placed on a uniform background, many of the early juveniles show quite an "inappropriate" body pattern (i.e. disruptive). Hanlon and Messenger (1988) observed that body patterns of juveniles become more and more adapted to uniform substrate in the course of post-embryonic development.

We confirm that almost all 1-day-old cuttlefish showed a chronic disruptive pattern both on variegated stones and uniform background. At hatching, however, the expression of this pattern seems to be relatively independent of the background (Poirier *et al.* 2005). When placed in an open field with four different substrates, a great majority of hatchlings will choose to stay on the contrasted and black substrates (Poirier 2004). We can hypothesize that in the sea, newly-hatched cuttlefish could avoid uniform or sandy substrates in favour of heterogeneous and/or dark backgrounds on which disruptive patterns seem to be better adapted.

In terms of learning and concealment abilities, the apparently poor behavioural plasticity in early juveniles could seem *a priori* curious since juvenile cuttlefish are very vulnerable to both predation and underfeeding. One can hypothesize that laboratory-rearing conditions may affect their behavioural maturation. To test this hypothesis, we undertook further studies to assess the influence of the rearing environment on behavioural and brain maturation in juvenile *Sepia*.

Phenotypic plasticity of behavioural development

Rearing environment plays a crucial role in behavioural and brain maturation in mammalian and avian species (reviewed in Renner & Rosenzweig 1987). These developmental traits are called "phenotypic plasticity" (West-Eberhard 1989). This crucial factor was rarely tested in invertebrate species. Cuttlefish appears to be a very relevant model for this kind of study: juveniles being totally autonomous from hatching, and rearing conditions being easy to control.

Predatory behaviour, learning and memory abilities

Among others, three groups of cuttlefish were reared in different conditions, namely standard laboratory conditions, SC (large and bare tanks, social conditions); impoverished conditions, IC (small bare tanks, solitary condition); and enriched conditions, EC (large tanks with sand, rocks, shells, seaweeds, social conditions). Using the "prawn-in-a-tube" paradigm, retention performance of the juveniles from groups SC, IC and EC were assessed at one and three months (Dickel *et al.* 2000). Early experience clearly influences both acquisition and retention performance of the learning task. At one month of age, cuttlefish reared in enriched conditions (group EC) displayed significant retention performance at 24 h whereas cuttlefish reared in impoverished conditions (group IC) and standard conditions (group SC) did not. The differences between groups at one month increased further at three months with the maturation rate of memory in cuttlefish from group SC, intermediate between group IC and EC. We have demonstrated that memory capacities appear related more closely to early experience than to cuttlefish size. In conclusion, memory formation in cuttlefish is greatly affected by the conditions under which the animals are reared; further data indicate that it occurs especially during the 2nd and/or 3rd months post-hatching (Dickel *et al.* 2000).

Defensive behaviour

Sand-digging behaviour

To determine whether development of sand-digging behaviour is subject to phenotypic plasticity, cuttlefish were individually reared from hatching in tanks with or without sand. Individuals of different ages were placed in a new tank, the bottom of which was covered with sand (Poirier *et al.* 2004). Cuttlefish previously reared on the sandy bottom showed shorter latencies of sand digging and covered themselves more completely than do cuttlefish reared in bare tanks. This finding indicates that the developmental changes in sand digging are, at least partially, experience-dependent. The presence of sand in rearing tanks would be a facilitating factor in sand digging maturation.

Body patterning

Cuttlefish were reared either in impoverished (IC) or enriched conditions (EC). At different ages, juveniles were individually placed, either on small variegated stones or on a uniform pale grey background (Poirier *et al.* 2005). In both groups, the number of disruptive animals remained high during the first two months of life when placed on a contrasted background. When placed on a uniform background, animals from both IC and EC showed a less and less disruptive pattern during the same period. However, to assess the efficiency of body patterns on uniform grey background, we determined the level of grey of each individual as a percentage of those of the background. The closer this percentage was to 100, the more the animal matched the background. On the contrasted background, the numbers of chromatic components were determined on each disruptive cuttlefish. The higher this number, the more efficient was the disruptive pattern. We have demonstrated that on both variegated and uniform backgrounds the efficiency of concealment increases during development. However, regardless of the juvenile ages, EC animals showed more efficient body pattern matching than IC animals. Therefore, cuttlefish rely not only on sensory inputs but also on their previous experience to display the appropriate body pattern for camouflage.

Early experience and brain maturation

A consideral body of literature exists on the influence of rearing environment on the central nervous system in mammals and birds (Mohammed *et al.* 2002). Even in arthropods, brain development has been linked to experience (Scotto-Lomassese *et al.* 2000, Punzo & Ludwig 2002). Dickel (1997) has shown that the vertical lobe complex develops faster in EC cuttlefish than in IC individuals, especially after the first month of life. These results appear consistent with those concerning the effect of rearing environment on memory development in juvenile cuttlefish (Dickel *et al.* 2000).

Body patterning is neurally controlled by the visual system (Messenger 2001). Using cell proliferation markers, we have shown that enriched rearing conditions increase cell proliferation in the optic lobes of young cuttlefish (Poirier 2004). In our experiments, cuttlefish were reared under the same lighting regime, but the enriched conditions probably provided enhanced visual stimulation, which may have optimized the maturation of the animal's visual system. Indeed, it would be interesting to go further into the study of the influence of rearing conditions on the maturation of the optic lobes.

The life of juvenile cuttlefish: from laboratory observations to the field (Fig. 1)

In the literature, data about early juvenile cuttlefish behaviour in the field are lacking. However, the data collected in laboratory conditions could lead us to a better understanding of how early juveniles could live under natural conditions.

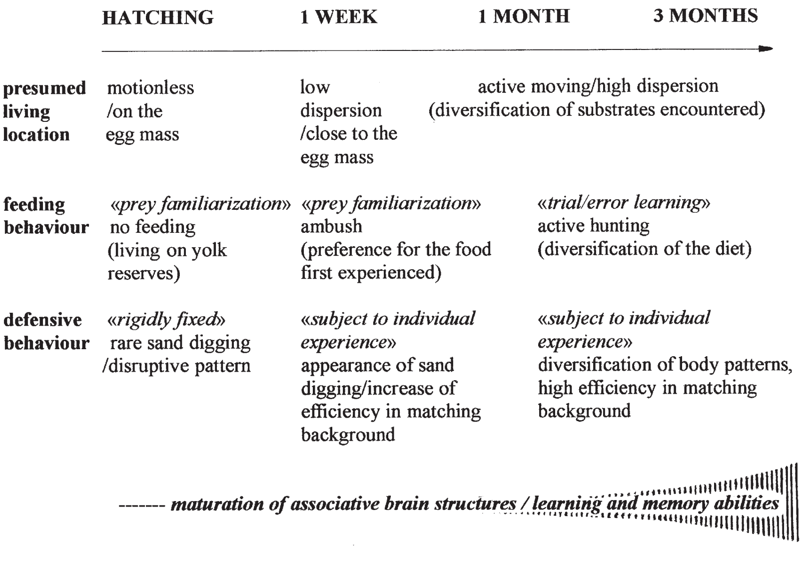

Fig. 1. – Time line illustrating the hypothetical development of cuttlefish behaviour in the field.

For the early hours following hatching, juveniles probably conceal themselves by showing relatively "stereotyped" disruptive patterns and rarely dig into the sand. They usually use the ventral surface of the mantle and ventral arms as a set of suckers to become firmly attached to hard and smooth substrates (Boletzky & Roeleveld 2000). In their environment of hatching, young cuttlefish may find an ideal, at the same time dark/contrasted and smooth/hard substrate: the egg mass itself. We have often observed in laboratory conditions that early juveniles, when allowed, usually remain directly on the eggs or in the immediate environment of the egg mass. We can easily imagine that the egg mass could constitute an efficient shelter against potential predators during this critical period.

Two additional arguments have to be put forward to support this hypothesis. Firstly, opaque egg envelops may provide the embryos with good visual and chemical protections, since eggs do not benefit from any parental protection (Guerra, *pers comm*). Hence predators generally do not take to interest in a cuttlefish's egg mass (Mangold 1989). Secondly, we have shown that hatchlings prefer contrasted, dark and smooth surfaces to any other ones (Poirier 2004). On this background (i.e. black egg surfaces in the field), disruptive patterns are probably efficient in concealing themselves. One can hypothesize that, while living on their yolk reserves, early juveniles would familiarize themselves with any potential prey present in their immediate environment. Their first meals could therefore be taken, ambushed, in the relative security of the egg mass. A "lie and wait" predation strategy does not require any prey-pursuit ability. During this period, the cuttlefish behaviour is probably largely driven by innate factors (substrate preference, body patterning, prey attractiveness…). After a few days, the young cuttlefish would leave their 'egg mass' shelter to begin their active predator life. In the course of these first weeks of life, their learning and retention abilities would progressively come into play, and they would diversify and optimize their diet probably by learning processes. As they grow, they will learn on which prey to feed and which to avoid. At the same time, the plasticity of their defensive behaviour will progressively increase, they will dig into the sand and, if necessary, begin to efficiently adapt their body patterns to different backgrounds. This phase will be associated with an important growth of their highly associative brain structures.

The results reported here have some implications for learning research using laboratory-cultured cephalopods. In terms of welfare as well as for studies of neural and behavioural maturation in cuttlefish, it seems that the rearing environment of the young should be carefully considered. In particular, the presence of the egg mass in their immediate environment, at least for the days after hatching, the presence of several types of prey, various backgrounds, shelters and obstacles (rocks, seaweed, etc.), the possibility of burrowing, could all potentially provide a better environment for the refinement of behaviour associated with defence and predation.

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