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Edited by Anne-Sophie Darmaillacq, Ludovic Dickel and Jennifer Mather

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Part I

Cognition, brain and evolution

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1 Cuttlefish preschool or how to learn in the peri-hatching period

Anne-Sophie Darmaillacq, Christelle Jozet-Alves, Cécile Bellanger and Ludovic Dickel

1.1 Introduction

One of the greatest challenges faced by many precocial young after hatching is that of finding food without being eaten. This challenge is particularly important in species where offspring receive no parental care. In these species, newly hatched young have at least two possible options in response to the problem of prey and predators: ‘come prepared’ (e.g. unlearned behaviour), which is safe but rigid, or ‘learn as you go’ (e.g. trial-and-error learning), which is risky if they do not learn quickly enough, but more flexible for adapting to a changing environment.

For a better understanding of how a newborn animal deals with environmental challenges, we need to study what is perceived and learned before hatching. Our understanding of prenatal cognitive activity is comparatively recent, compared for example with philosophical trends of the seventeenth century. A cognitive system can be defined as one which is able to perceive and extract information from its environment, and then use that information for the purpose of making appropriate decisions and developing suitable behaviour (Shettleworth, 2010; Vauclair, 1996). There is no longer any doubt about the embryo as a cognitive system, since it is now well established that fetal sensory experience has a crucial role in behavioural and cognitive development (Krasnegor, Blass, Hofer & Smotherman, 1987).

Although there are 700 cephalopod species, the common cuttlefish *Sepia officinalis* has been the focal subject of intensive developmental studies in neuroethology. Cuttlefish, like many other cephalopod species, start life under strong selective pressure from their environment; neither eggs nor juveniles benefit from parental care (Boletzky, 1987), and so young individuals must find their own means of feeding themselves and avoiding predators. Female *S. officinalis* lay hundreds of eggs in shallow water on various rigid supports: algae stems, tubeworms, ropes, nets, etc. (Boletzky, 1983). Eggs laid in clusters, popularly known as ‘*les raisins de mer*’ (sea grapes), are abandoned after the death of the mother. The egg capsule consists of a chorion and spirally coiled black envelopes, which protect the embryos against microbial attack and predation (Boletzky, 2003). Throughout embryonic development, the capsule is enlarged as osmotic pressure increases due to water entering the perivitelline space, becoming more translucent shortly before the

embryos hatch. Once the animals have hatched, egg envelopes decay after some weeks of degradation (Billings, Sullivan & Vine, 2000). Unlike many other cephalopods, there is no larval or paralarval stage in cuttlefish development; the hatchlings are very similar to adults in their general form, which facilitates comparative development studies. They possess the same benthic life style as adults; they can also swim in the water column, achieve elaborate forms of crypsis by colour pattern and posture changes, and use the same prey-catching strategies as adults, by striking out with their tentacles or by jumping on prey. They seem to possess a behavioural repertoire comparable with that of adults, although some adjustments in both predatory and defensive behaviour occur during development (for review, see Dickel et al., 2006). The brain of early juveniles has the same structure as that of adults, and all the brain lobes are present from hatching. Neurogenesis is intense during development (e.g. in octopus, the adult brain possesses a thousand times more neurones than that of the hatchling) and some brain structures develop faster than others during post-embryonic maturation (for a review, see Nixon & Young, 2003). From an experimental point of view, these characteristics make the cuttlefish a unique animal model in developmental neuroethology; firstly, because the absence of parental care allows a precise control of the experiential history of embryo and juvenile; and, secondly, because the absence of a paralarval stage in young cuttlefish allows longitudinal and comparative studies of brain and behaviour from hatching to adulthood.

This chapter is a review of the most recent studies addressing the influence of early experience in *S. officinalis*, from embryonic stages, to post-hatching behaviour and cognition. It will first describe the development of the sensory systems and the central nervous system in the embryo. It will then focus on the factors affecting the development of prey preference and the efficiency of primary defences in newly hatched cuttlefish and juveniles. It will also address the ontogeny of lateralization in cuttlefish, which may afford juveniles greater behavioural efficiency by enabling them to look out for escape routes while hunting. Finally, we will try to describe the scenario of the beginning of the life of a cuttlefish.

1.2 Development of the sensory systems

The study of cognition is concerned with how animals process information, beginning with how information is acquired by the senses (Shettleworth, 2010). As all of an animal's experience is founded on its ability to sense changes in its environment, measurement of the embryo's sensory capabilities allows us to define the limits of its potential for modifying its behaviour through experience (Smotherman & Robinson, 1992). The onset of sensory system function follows an invariant sequence in birds and mammals – i.e. tactile, vestibular, chemical, auditory and visual (Gottlieb, 1971; Lickliter, 1993). This process remains to be investigated in invertebrates. The sense organs of adult cuttlefish have been well described (Hanlon & Messenger, 1996), but we do not know at what point they begin to function during embryonic development. The stages of embryonic development in the cuttlefish have been precisely described by Lemaire (1970), from

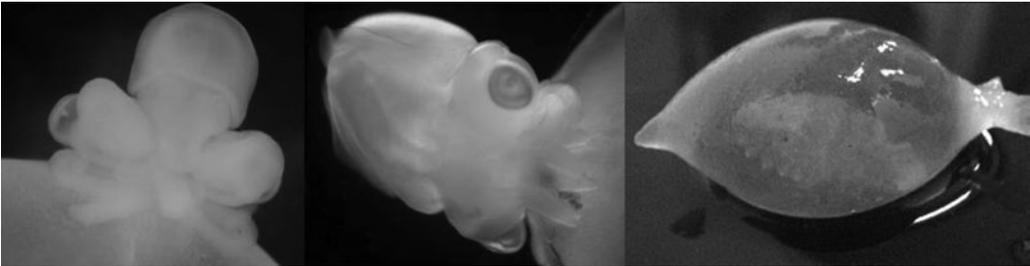


Figure 1.1 *Sepia officinalis* embryonic stages according to Lemaire (1970) from left to right: (A) stage 23, (B) stage 25 and (C) stage 30 (copyright L. Bonnaud and A.-S. Darmaillacq). See plate section for colour version.

segmentation to organogenesis. Organogenesis ranges from stage 18 to stage 30 (i.e. hatching). From stage 23 (about 4 weeks before hatching, incubation temperature 18°C, embryo size about 1 mm; Figure 1.1, left), rhythmic mantle contractions are visible through the outer covering of the egg (Romagny, Darmaillacq, Guibé, Bellanger & Dickel, 2012); stage 25 (about 3 weeks before hatching, incubation temperature 18°C, embryo size about 2 mm; Figure 1.1, middle) is easily identifiable by the reddish colouration of the retina and stage 30 (a few days before hatching, incubation temperature 18°C, embryo size from 7 to 9 mm; Figure 1.1, right), corresponds to the hatching stage where embryos resemble juveniles (Lemaire, 1970).

Variations in the frequency of mantle contractions in adult cuttlefish have been demonstrated to be a good indicator of stimulus detection (odour: Boal & Golden, 1999; visual stimuli: King & Adamo, 2006). Romagny, Darmaillacq, Guibé, Bellanger & Dickel (2012) used this behavioural characteristic to investigate whether tactile, chemical and visual sensory systems are functional in cuttlefish embryos. From stage 23, these authors observed an increase of the rate of mantle contractions immediately after a gentle prick on the ventral mantle of the embryo with a blunt needle through the membrane of the egg. At the same developmental stage, a predator odour introduced to the immediate environment of the egg induces the same behavioural response. Response to visual stimuli (sudden light) did not occur earlier than stage 25. This study shows for the first time that in cuttlefish sensory systems do not all become functional at the same stage of embryonic development. As in vertebrates (Lickliter, 1993), visual system maturation in the cuttlefish embryo occurs later than that of the tactile and chemical systems. This similarity between cuttlefish and vertebrates could merely be a coincidence but it could also suggest a unique evolutionary origin or, more likely, a similar convergent evolution. The latter hypothesis is reinforced by the other known evolutionary convergences between the sensory systems of cephalopods and vertebrates (e.g. eyes, statocysts, lateral line; Budelmann, 1994; Nixon & Young, 2003; Packard, 1972). Similar environmental pressures could have led to the same developmentally conserved sequence in vertebrates and in invertebrates. Further investigation on behavioural embryology in invertebrates could provide important insights into whether this phenomenon is conserved throughout different taxa.

One expression of structural and functional developments in the sensory systems of embryos is the ability to learn. Three types of learning have been documented, mainly in vertebrates, as originating from prenatal sensory stimulation by chemosensory and auditory stimuli: these are habituation, associative learning and exposure learning. Associative and exposure learning can only be assessed after hatching even if the process of acquisition occurs before hatching (see section 1.3.5) whereas habituation can be directly tested with embryos. Habituation, understood to be a simple form of learning, is defined as a decreasing response to an often-repeated stimulus. This has been demonstrated in mammal fetuses (Granier-Deferre & Busnel, 1983; van Heteren, Boekkooi, Jongsma & Nijhuis, 2001; Schaal, 1988; Smotherman & Robinson, 1992). In *S. officinalis* embryos, habituation to a light stimulus presented every 30 minutes occurs at stage 30 but not at stage 25 (Romagny, Darmaillacq, Guibé, Bellanger & Dickel, 2012). This learning is disrupted with a dishabitatory stimulus (a prick). Habituation is a central process which allows the subject to filter irrelevant information and focus on biologically meaningful stimuli. Before the egg capsule dilates and becomes transparent, the embryo develops in a visually buffered dark environment, in which light is attenuated by the capsule before reaching the developing embryo. This may explain why the visual habituation processes are not mature at stage 25. In the experiments described above, the outer dark layer of the eggs was removed. It, therefore, seems likely that habituation to tactile or chemical stimuli can occur before stage 30. There is a rich and varied array of stimuli in the prenatal environment and so it seems likely that the embryos would make ‘sense’ of these opportunities for learning about their future world. Firstly, a decrease of the response to repeated non-relevant stimuli may serve the embryo to avoid loss of energy. Secondly, its capabilities to memorize visual information from the environment perceived in the egg may potentially optimize behavioural adaptation of hatchlings to environmental pressure met at the hatching sites (available shelters, predators and prey).

1.3 Early learning about prey

1.3.1 Prey preference and early experience

Cuttlefish are active predators, feeding on different types of prey including fish and crustaceans (Guerra, 2006). They search for prey and find it mainly by visual means (Messenger, 1968), although one cannot exclude the possibility that other sensory means may be involved, and prey movement is of real significance. The question is: how do newly hatched cuttlefish recognize safe prey in the absence of parental assistance and/or observational learning? Wells (1962) presented newly hatched cuttlefish having no prior post-embryonic experience of food with a series of models, either rotating or moving up and down, to newly hatched cuttlefish without prior post-embryonic experience with food. He showed that they preferred elongate shapes moving along their longer axis (mysid-like prey) to rounded shapes (crab-like prey) that they almost never attacked.

Unfortunately Wells (1962) did not actually record the environmental conditions in which the eggs developed, conditions that might have influenced prey choice. When naïve 1-day-old cuttlefish are given a choice between shrimp, crabs and fish, again they prefer shrimp to the other two types of prey (Darmaillacq, Chichery, Poirier & Dickel, 2004). This finding not only confirms that cuttlefish have an innate preference for shrimp-like prey. It also suggests that prey recognition is based on identification processes of a higher order than the simple selection of elongate prey moving along their long axis, since hatchling cuttlefish prefer shrimp to fish which nevertheless share the same basic characteristics. This preference for shrimp continues throughout the first month of life but then seems to extend to other prey types even when cuttlefish are only fed shrimp. It is known that early experience exerts a particularly potent influence on subsequent food selection. For example, turtles retain a preference for the first food they experience in their life (Burghardt, 1967; Burghardt & Hess, 1966). This phenomenon, known as the primacy effect, has also been shown in other precocial species such as the lynx spider (reviewed in Stasiak, 2002 and see also Punzo, 2002). In cuttlefish, Darmaillacq, Chichery, Poirier & Dickel (2004) showed that juveniles that ate crab as their first meal 3 days after hatching subsequently preferred crabs to shrimp. The ability to learn the positive consequences of food ingestion may be adaptive to a young animal needing to select safe prey alone. However, it may be a risky option for the young to be genetically programmed to seek out a single type of prey, especially in the case of a changing environment.

1.3.2 Associative learning

Cuttlefish actively prey upon shrimp, capturing them by shooting out their two tentacles for a strike. This behaviour, visually driven, has been extensively used in the studies of learning and memory capabilities in cuttlefish since the 1940s. Shrimp are presented behind glass (or inside a glass tube; Figure 1.2); the cuttlefish then attacks the prey but does not obtain it (Agin, Chichery & Chichery, 2001; Agin, Chichery, Maubert & Chichery, 2003; Bellanger, Dauphin, Chichery & Chichery, 2003; Dickel, Boal & Budelmann, 2000; Dickel, Chichery & Chichery, 1997, 1998, 2001; Messenger, 1971; Sanders & Young, 1940; Wells, 1962).

Under these conditions, *S. officinalis* learns not to attack the shrimp and, hence, to inhibit the predatory motor pattern: the number of capture attempts (tentacle strikes) decreases with stimulus presentations. This learning has been recognized as a form of associative learning (Agin, Dickel, Chichery & Chichery, 1998; Agin et al., 2006; Messenger, 1973). Following a massed procedure (a single continuous 20-min training phase), with various retention times (between 2 min and 2 days), Messenger (1971) reported differential performance of memory recall in adult cuttlefish. He considered this retention curve to be a product of two memory stores: a labile short-term memory (STM) lasting for a period of some minutes, and a long-term memory (LTM) lasting at least 2 days, and probably more. The retention curves obtained in 30- and 90-day-old cuttlefish bear a close resemblance to those recorded in adults, suggesting that LTM is

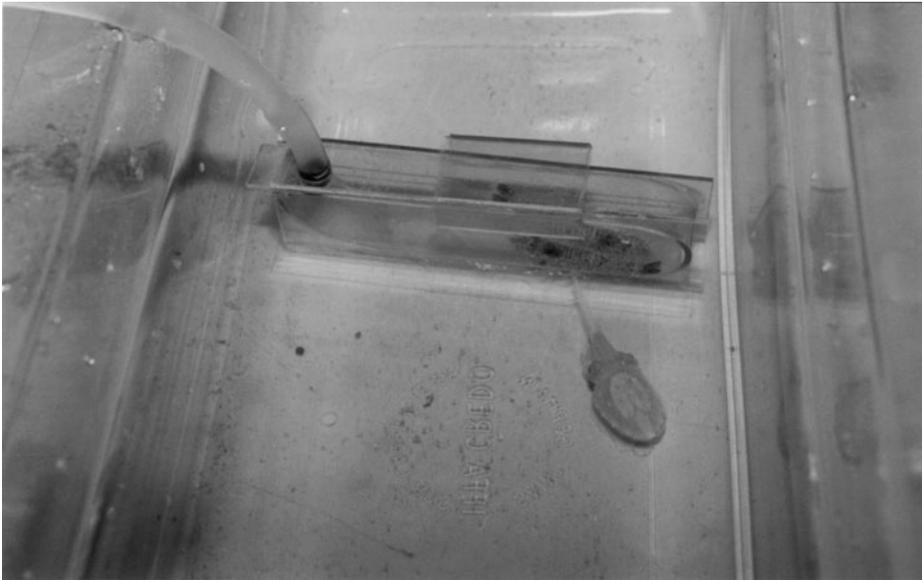


Figure 1.2 One-week-old cuttlefish striking at shrimp enclosed in a glass apparatus. The prey movement is kept constant by a continuous water flow (copyright L. Dickel).

fully operational from one month of age (Agin et al., 2006). STM appears earlier, as early as 8 days of age (Dickel, Chichery & Chichery, 1998), but 1-week-old cuttlefish have poor 60-minute retention performance. This improves progressively between 15 and 60 days of age (Dickel, Chichery & Chichery, 1998). These results suggest that there is a time lag between the establishment of short- and long-term memory systems during post-embryonic development and that LTM matures later than STM. Moreover, there is an improvement in the acquisition of learning ability during the first 2 months of life, as well as an increase of 24-hour retention performance between 30 and 90 days of age (Dickel, Boal & Budelmann, 2000; Dickel, Chichery & Chichery, 2001). As first suggested by Wirz (1954), this poor LTM performance in 8-day-old cuttlefish has been related to the immaturity of the brain's vertical complex (see below, section 6). This is particularly true of the vertical lobe, which, although the smallest lobe of the vertical complex at hatching, nearly doubles in size during the first month of post-embryonic development (Dickel, Chichery & Chichery, 1997, 2001).

However, this seems in contradiction with the findings of Darmaillacq, Chichery, Poirier & Dickel (2004) where cuttlefish fed on crab at 3 days of age, subsequently showed a preference for crab rather than their naturally preferred prey 4 days later. One can imagine that it is much more adaptive for a growing individual to learn quickly that available food is a positive alternative when their naturally preferred food is not accessible. Another possibility, not mutually exclusive with the first, is that such learning depends on different mechanisms and involves different brain structures than those involved in the retention of an associative task. This point will be discussed later in this chapter.

1.3.3 Food imprinting

Cuttlefish hatch with internal nutritive reserves. Even if active predation can begin before the inner yolk is entirely used up (Boletzky, 1987; Dickel, Chichery & Chichery, 1997), these reserves allow young cuttlefish to go without food for a few days. This period is probably critical in the life of young cuttlefish, since hatchlings can collect information about their environment (potential food, predation risk, shelters) before they start foraging. In cuttlefish from the English Channel, the prey-pursuit behaviour does not begin before the end of the first week after hatching (Dickel, Chichery & Chichery, 1997). From these data, it has been shown that the preference for crabs could be induced simply after visual familiarization with them during a sensitive period within the first hours of life after hatching (Darmaillacq, Chichery & Dickel, 2006; Darmaillacq, Chichery, Shashar & Dickel, 2006).

Interestingly, the efficiency of this familiarization depends on the length of the exposure as well as the density of prey exposed, i.e. the flow of information perceived during the sensitive period. Finally, it appears that the primacy of the early familiarization outweighs the untrained preference for shrimp (Darmaillacq, Chichery, Shashar & Dickel, 2006). This learning of the visual characteristics of a potential prey meets all the criteria of imprinting (Sluckin, 2007): no reinforcement, sensitive period, persistence (Darmaillacq, Chichery, Shashar & Dickel, 2006) and generalization (Guibé, Poirel, Houdé & Dickel, 2012; see next section). Food imprinting could account for the prey preference observed in 1-week-old cuttlefish, an effective compromise between the flexible but precarious strategy of trial and error, and the rigid, genetically driven response of non-learning. Such early learning capabilities would allow juveniles to take advantage of a changing environment and to deal with a world where shrimp (i.e. their “innate” food preference) was unavailable. To our knowledge, there is no available literature about fluctuation in prey availability on the English Channel coasts. Unlike filial or sexual imprinting, food imprinting might seem ineffective and even disadvantageous in the long term (Healy, 2006), in particular for long-lived individuals in a changeable environment. However, it could be helpful for juveniles to find available prey attractive in the weeks following hatching before they begin to forage.

It also appears that, if we compare these results with those obtained from the prawn-in-the-tube protocol, the two different types of learning may depend on the presence of different neural substrates.

1.3.4 Prey generalization

The preference for different types of prey observed in cuttlefish suggests that they are capable of interspecies discrimination (crab vs shrimp). Both crab and shrimp belong to the Class Crustacea, but they differ greatly in characteristic movement and morphology. A recent study has shown that naïve hatchlings preferred black crabs to white ones (Guibé, Poirel, Houdé & Dickel, 2012); this result is consistent with those obtained in the adult octopus, which spontaneously prefers to attack dark over white artificial objects (Fiorito & Scotto, 1992; Messenger & Sanders, 1972). However, if newly hatched

cuttlefish have been exposed to white crabs, their spontaneous preference changes to white crabs. This demonstrates that cuttlefish have the ability to discriminate between two crabs from the same species but with different cephalothorax luminance. Moreover, if they are familiarized with white crabs at hatching, they subsequently prefer black crabs to shrimps. This means that they can generalize the learning of the characteristics of a prey to which they have been familiarized to a novel prey that shares some morphological features (Guibé, Poirel, Houdé & Dickel, 2012), and suggests a capacity for prey-generalization and possibly categorization in hatchling cuttlefish. This cognitive process, which consists in grouping distinguishable objects or events on the basis of a common feature or set of features and consequently to respond in a similar way to new stimuli, is a cognitive economy. Perceptual categorization has been extensively studied in pigeon, monkeys and honeybees using operant conditioning (Wasserman & Zentall, 2006), but still poorly investigated in marine molluscs.

It should be mentioned here that late juvenile cuttlefish (dorsal mantle length, DML, from 100 to 140 mm) from the wild systematically catch crabs (cephalothorax length, CL, from 40 to 60 mm) by the jumping strategy, although they capture shrimp by striking with their tentacles (Chichery, 1992). Results show that fewer than 60% of crab captured by inexperienced 5-day-old cuttlefish are caught by the jumping strategy (Dickel, 1997). These observations show that, even though crab identification is possible at hatching, there seems to be a correlation between the decision-making processes for catching prey and the experience and/or later brain maturation of juvenile cuttlefish. The frequency with which the jumping strategy is adopted in crab predation increases progressively during post-embryonic development to reach more than 80% after a month of life (Dickel, 1997). A possible hypothesis is that the later maturation of the vertical lobe system is a factor in these processes (see below).

1.3.5 Embryonic learning of visual features of potential prey

In *S. officinalis*, the egg envelopes are stained black with the ink of the female. As the embryo grows and the osmotic pressure of the perivitelline fluid increases (Boletzky, 1983), the elastic envelopes are dilated and some parts peel off so that the envelopes become more transparent. By the end of embryonic development the tactile, chemical and visual systems are all functional (see above, section 1.2), so that it is very likely that the embryo approaching the end of its development can perceive stimuli coming from its environment and, in particular, potential prey. Darmaillacq, Chichery, Shashar & Dickel (2006) showed that the sensitive window for food imprinting was open at hatching; given the characteristics of the egg capsules and the embryo's cognitive competencies, this sensitive period is likely to begin before hatching. Based on this assumption, Darmaillacq, Lesimple & Dickel (2008) exposed cuttlefish embryos to crabs for at least a week before hatching (Figure 1.3). They were able to show that these cuttlefish subsequently preferred crab to shrimp, unlike a control group of cuttlefish that had not seen crab during the sensitive period before hatching. Hence, embryos are able to learn the general shape of a potential prey in the late stages of their development. This preference was observed whether the outer layer of the egg envelope had been removed or not.