



Embryonic visual learning in the cuttlefish, *Sepia officinalis*

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The ability to learn about chemosensory stimuli in the prenatal period is now well established in a wide variety of vertebrate species. This may help to shape development and behaviour. Evidence for early visual learning has already been shown in newly hatched cuttlefish. We exposed cuttlefish embryos to crabs for at least a week before hatching. This crab exposure induced a subsequent visual preference for crabs in 7-day-old juveniles. The results show for the first time embryonic visual learning in animals. Such cognitive abilities in embryos that can perceive visual stimulation could confer important adaptive advantages in processing and acquiring information about foods likely to be available after hatching.

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Since the 17th century philosopher John Locke's idea that newborn children can be considered to be blank slates at birth, research has repeatedly confirmed the crucial role of fetal sensory experience in behavioural and cognitive development (Smotherman & Robinson 1992; Alberts & Ronca 1993; Chapillon et al. 2002). Extensive studies of fetal behaviour have shown learning after a single exposure to chemosensory stimuli (humans: DeCasper & Spence 1986; Schaal et al. 2000; Mennella et al. 2001; rats, *Rattus norvegicus*: Hepper 1988, 1990; dogs, *Canis familiaris*: Wells & Hepper 2006) and both associative and nonassociative learning (Rudy & Cheatle 1977; Smotherman 1982; Smotherman & Robinson 1992; Hepper 1997; Gruet et al. 2004; Kawai et al. 2004). Overall, these studies suggest that prenatal sensory experience influences postnatal behaviour. Besides mammals, prenatal learning has been recorded in a wide variety of species (auditory imprinting: birds: Gottlieb 1976; Impekoven 1976; Shindler 1984; chemosensory learning: birds: Sneddon et al. 1998; reptiles: Sneddon et al. 2001; fish: Brannon 1972; amphibians: Hepper & Waldman 1992; insects: Isingrini et al. 1985; Caubet et al. 1992).

Most of the studies mentioned above investigated prenatal exposure learning based on chemical or auditory stimulation, the most likely cues to pervade the embryo's

environment. They suggest that individuals prefer the stimulus to which they have been exposed before birth to an unfamiliar one. The widespread occurrence of prenatal sensory learning means that it may be critical to the individual's survival in the perinatal period, for example for mother and kin recognition or feeding behaviour (Hepper 1996; Coureaud et al. 2002). This also emphasizes the importance of prenatal external influences in the development of behaviour (either the mother's influence in mammals or the stimuli present within an ecological niche). As for prenatal visual stimulation, investigations in reptiles and birds showed that stimulation such as patterned light presented during the late prenatal period alters incubation times and postnatal auditory preferences (leopard geckos, *Eublepharis macularius*: Sleigh & Birchard 2001; bobwhite quails, *Colinus virginianus*: Honeycutt & Lickliter 2002). However, no studies of prenatal visual learning per se have been conducted in any vertebrate models so far, because visual cues are unlikely to be experienced by the embryos of mammals and birds.

Among invertebrates, cuttlefish (a cephalopod mollusc) are suitable models for the study of development (reviewed in Dickel et al. 2006), and they rely strongly on vision in several aspects of their life history. For example, their predatory behaviour (Messinger 1968) and their defensive behaviour (e.g. body patterning) are mediated by the visual system (Hanlon & Messenger 1988; Chiao & Hanlon 2001). The eggs and the newly hatched young do not benefit from parental care so that the latter have to search autonomously for their own food after hatching.

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Last, the spirally coiled envelopes of the eggs are stained in black with ink. During late embryonic development, however, the elastic envelope is dilated by the increase in osmotic pressure of the perivitelline fluid (von Boletzky 1983) so that it becomes more transparent. Examination of the late embryonic stages showed that the structure of the eyes is by then fully developed (Lemaire 1970).

There is evidence that the cuttlefish, *Sepia officinalis*, is able to learn in the immediate posthatch period. Postnatal visual exposure to crabs (a naturally nonpreferred prey) induced a significant change in the juvenile's initial food preference (Darmaillacq et al. 2006a). This learning was subsequently characterized as being food imprinting (Darmaillacq et al. 2006b). Then, one question arises: are cuttlefish embryos able to learn about the visual characteristics of the prey present in the environment before hatching?

We examined the effect of early embryonic exposure to crabs on subsequent prey preferences in *S. officinalis* juveniles and then addressed to what extent the envelope of the egg is a barrier to the perception of the immediate environment of the eggs.

METHODS

Study Animals

We used eggs laid by wild-caught females obtained from trawling off Luc-sur-Mer, Calvados, France and kept in large tanks (1500 litres) at the CREC (Centre de Recherches en Environnement Côtier), Luc-sur-Mer, France. Females were fertilized either before they were caught or after mating in the tanks at the CREC. Eggs, initially laid in clusters that females attached to plastic meshes available in the tanks, were separated to ensure optimum development conditions and were put in shallow tanks. All tanks were supplied with running oxygenated sea water ($18 \pm 1^\circ\text{C}$). As prey, we used crabs, *carcinus* sp. (carapace width 2–3 mm) and shrimps, *Crangon crangon* (1 cm long).

Apparatus: Crab Exposure to Embryos

The experimental apparatus allowed controlled exposure to the crabs (Fig. 1). The experimental tanks (each 21×4 cm and 8 cm high) were made of opaque plastic. Each contained two internal, closed, elevated compartments running along each of the long sides into which we placed the crabs. The bottom and top of each elevated compartment were opaque and the inward faces were of clear glass to prevent the crabs escaping into the water but to allow their exposure to the embryos. This was also designed to prevent the embryos or the newly hatched cuttlefish perceiving chemical cues from the crabs. The side walls of each tank, below the elevated compartments, were perforated so that the sea water could circulate freely without allowing hatchlings to escape.

In each experimental tank a maximum of 10 eggs were suspended from a nylon thread running along the centre line between the side compartments, the distal tips of the eggs being aligned with the lower edge of the raised

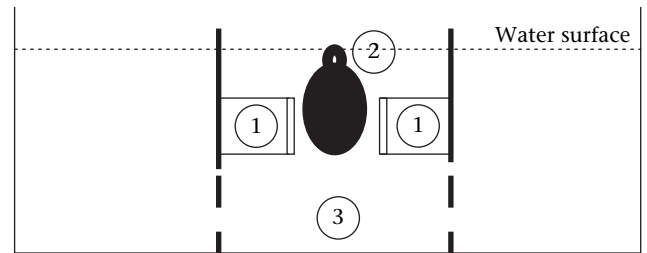


Figure 1. Cross-section of the experimental apparatus to allow controlled exposure of crabs to the embryos. (1) Crabs were placed in opaque-bottomed, glass-fronted compartments with closed sides separated from the cuttlefish eggs. (2) The eggs were suspended lengthwise between the side compartments. (3) Newly hatched cuttlefish fell into the area, below the elevated compartments, from which the crabs were no longer visible. The apparatus was bottomless and placed in a larger tank to allow us to collect the newly hatched cuttlefish.

compartments so that the embryos (positioned head down in the eggs) could see the crabs. Once prepared, the experimental tanks were placed in a larger sea water tank (100 × 150 cm and 10 cm high; Fig. 1).

Procedure

Eggs were assigned to one of three groups and arranged in the experimental apparatus described above. Eggs of group 1 (G1; $N = 24$) were exposed to crabs (25 crabs in each of the two side compartments). Eggs of group 2 (G2; $N = 24$) received the same treatment as G1 except that we removed the outer layers to make the envelope more transparent. As a control, eggs of group 3 (G3; $N = 20$) were arranged in the same experimental apparatus but were not exposed to crabs.

When they hatched, the cuttlefish fell below the side compartments so that they were no longer exposed to the crabs (Fig. 1). Since cuttlefish usually hatch at night (Paulij et al. 1991) they were collected in the morning (day 0) and isolated in individual, perforated, opaque plastic tanks (7×8 cm and 8 cm high) supplied with running sea water at $18 \pm 1^\circ\text{C}$. Juveniles were not fed and did not see or 'smell' any prey until day 7, the day of testing; they can endure a week of fasting because they still have inner nutritive reserves (von Boletzky 1975, 2003; Dickel et al. 1997). On day 7, we assessed their visual prey preference in a two way choice between crabs and sand shrimps (apparatus and procedure detailed in Darmaillacq et al. 2004). We recorded a preference for a prey when the cuttlefish carried out the visual attack sequence, ending in the cuttlefish being positioned in front of the corresponding compartment and about to attack the prey (Messenger 1968). Since cuttlefish usually attack prey within 1 min, we allowed the juvenile 5 min to make a choice. Beyond this time, we considered that the cuttlefish did not choose. We then recorded whether cuttlefish in each group preferred crabs or shrimps or made no choice. For half of the trials, crabs were presented in the left-hand compartment and for half in the right-hand one, alternately with shrimps. Each cuttlefish was tested individually and used only once.

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