

RESEARCH ARTICLE

Maturation of polarization and luminance contrast sensitivities in cuttlefish (*Sepia officinalis*)

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SUMMARY

Polarization sensitivity is a characteristic of the visual system of cephalopods. It has been well documented in adult cuttlefish, which use polarization sensitivity in a large range of tasks such as communication, orientation and predation. Because cuttlefish do not benefit from parental care, their visual system (including the ability to detect motion) must be efficient from hatching to enable them to detect prey or predators. We studied the maturation and functionality of polarization sensitivity in newly hatched cuttlefish. In a first experiment, we examined the response of juvenile cuttlefish from hatching to the age of 1 month towards a moving, vertically oriented grating (contrasting and polarized stripes) using an optomotor response apparatus. Cuttlefish showed differences in maturation of polarization *versus* luminance contrast motion detection. In a second experiment, we examined the involvement of polarization information in prey preference and detection in cuttlefish of the same age. Cuttlefish preferentially chose not to attack transparent prey whose polarization contrast had been removed with a depolarizing filter. Performances of prey detection based on luminance contrast improved with age. Polarization contrast can help cuttlefish detect transparent prey. Our results suggest that polarization is not a simple modulation of luminance information, but rather that it is processed as a distinct channel of visual information. Both luminance and polarization sensitivity are functional, though not fully matured, in newly hatched cuttlefish and seem to help in prey detection.

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INTRODUCTION

Visual motion detection plays a crucial role in the early life stages of many organisms, as it is used for predator avoidance [fish (Fuiman and Magurran, 1994)] and prey detection [fish (Luczkovich, 1988); birds (Gall and Fernández-Juricic, 2010)]. Although motion detection itself is a fundamental trait, occurring with the establishment of visual functions, the acuity of vision and hence the ability to detect small patterns often changes with age and mostly with increase in eye size (Pankhurst et al., 1993; Kiltie, 2000). The optomotor response (OMR) is the unconditioned movement (of the whole body or the head) exhibited by an individual [from insects to humans (McCann and MacGinitie, 1965; Tauber and Koffler, 1966)] when it is presented with a large-field moving stimulus. Experimentally, this behavior is induced by placing the animal inside a rotating cylinder lined with a pattern made up of contrasting stripes. The OMR has been used to study the ontogeny of visual functions in many animal species (Rahmann et al., 1979; Neave, 1984; Carvalho et al., 2002; Groeger et al., 2005; Rinner et al., 2005) because it allows the testing of a large variety of parameters such as spatial resolution (the capacity to discriminate details) and temporal resolution (the capacity to detect motion). For this purpose, the size of the stripes of the pattern on the rotating cylinder and/or the velocity of rotation can be varied. The OMR allows examination of spectral sensitivity (Cronly-Dillon and Muntz, 1965; Kaiser, 1974; King et al., 1993; Krauss and Neumeyer, 2003) as well as polarization sensitivity (PS) (McCann and Arnett, 1972; Wolf et

al., 1980; Philipsborn and Labhart, 1990; Dacke et al., 2001; Glantz, 2001).

Cephalopods are colorblind (Brown and Brown, 1958; Hanlon and Messenger, 1996; Marshall and Messenger, 1996; Mäthger et al., 2006). Yet in addition to their contrast sensitivity (grey scale), they are sensitive to the linear polarization of light, a sensitivity that arises from the orthogonal distribution of the microvilli of neighboring photoreceptor cells in their retina (reviewed in Mäthger et al., 2009). PS is the capacity to respond to changes in either the *e*-vector orientation (also known as angle of polarization) or the degree of polarization (also referred to as percent polarization or partial polarization) of a light stimulus (Wehner, 2001; Horvath and Varju, 2004; Marshall and Cronin, 2011). Cuttlefish respond to differences as small as 1 deg (Temple et al., 2012) and thus have highly acute *e*-vector angle discrimination capacities. In addition to its use in target detection by octopus and squid (Moody and Parriss, 1960; Moody and Parriss, 1961; Shashar et al., 1998), PS is used by cuttlefish in a range of tasks such as communication (Shashar et al., 1996; Boal et al., 2004), predation (Shashar et al., 2000) and orientation (Cartron et al., 2012). Cuttlefish are visually driven predators that prey upon various small moving crustaceans (Hanlon and Messenger, 1996). Of them, mysid shrimp use transparency for camouflage (Wells, 1962) but their tissues generate localized polarization *via* scattering, reflection and birefringence, which could allow polarization-sensitive predators detect them (Johnsen et al., 2011). Likewise, adult cuttlefish use PS to detect silvery fish

that also generate a polarization pattern (Shashar et al., 2000). Other prey, such as crabs, use contrasted pattern of coloration to mimic the background (Todd et al., 2006).

Newly hatched cuttlefish do not benefit from parental care so they need to cope on their own to hunt such silvery and transparent prey (Boletzky et al., 1977). Therefore, it is of interest to examine the ontogenetic development of polarization-based visual capacities and to compare them with luminance contrast-based visual capacities. OMR induced in juvenile *Sepia officinalis* improved in luminance-contrast-based visual acuity from a minimum separated angle of 2.5 deg in cuttlefish measuring 1 cm to 0.5 deg for cuttlefish measuring 8 cm (Groeger et al., 2005). OMR was also used to examine PS in adult cuttlefish of different species, but has not yet been studied in hatchlings (Darmaillacq and Shashar, 2008; Talbot and Marshall, 2010a; Talbot and Marshall, 2010b). Newly hatched cuttlefish are able to visually discriminate between different crab phenotypes, suggesting good detection of prey based on luminance contrast (Guibé et al., 2012).

In the present study, we used both OMR and predatory behavior to examine and to compare the development of polarization and luminance contrast sensitivities in young cuttlefish, from hatching to 1 month of age. In the first experiment, we observed the OMR to polarization and luminance contrasted patterns in motion. Then, in the second experiment, we examined the importance of polarization information in detecting and attacking prey that use transparency or background matching as camouflage (Stevens and Merilaita, 2009).

MATERIALS AND METHODS

Animals

Cuttlefish *Sepia officinalis* Linnaeus 1758 were hatched from wild eggs collected in the vicinity of Luc-sur-Mer, France. Eggs, initially

laid in clusters, were separated from each other to ensure optimum developmental conditions and were put in shallow tanks at the Centre de Recherches en Environnement Côtier (CREC, Luc-sur-Mer, France). All tanks were supplied with running oxygenated seawater at $17\pm 1^\circ\text{C}$. After hatching, the animals were housed in groups and provided with enriched habitats, which increases cuttlefish growth rates, has a positive effect on juveniles' learning abilities (Dickel et al., 2000) and improves the richness of their behavioral repertoire (Poirier et al., 2004; Poirier et al., 2005). Animals were fed daily with live shrimp (*Crangon crangon*) of suitable size. After being tested, cuttlefish younger than 1 month were released into their natural environment at low tide in shallow pools containing potential prey and hiding places (Darmaillacq et al., 2006; Darmaillacq et al., 2008). Older animals were kept in the rearing system for further, unrelated, experimentation.

Two experiments were conducted. The first experiment tested an unconditioned response to geometrical moving stimuli (OMR). The second experiment tested predatory behavior in a biologically relevant context.

Experiment 1: OMR to luminance versus polarization contrasted patterns

Apparatus

We used an optomotor apparatus consisting of a cylinder (26 cm in diameter, 21 cm high) rotated by a controllable, reversible motor as described in detail in Darmaillacq and Shashar (Darmaillacq and Shashar, 2008) (Fig. 1A). The interior wall of the cylinder was lined with one of the removable striped patterns while the exterior was backed with a light diffuser. A circular glass holding tank (8 cm in diameter, 8.5 cm high; Fig. 1A) was placed on a central stationary platform. A video camera was suspended directly above the glass

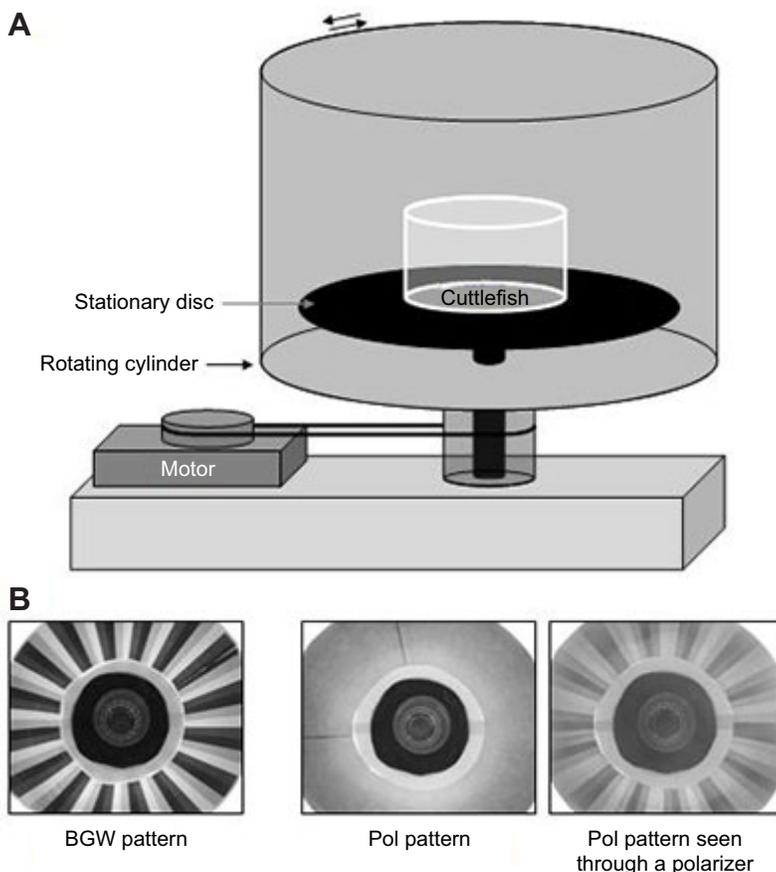


Fig. 1. (A) Optomotor apparatus. (B) Photos taken from above of the BGW pattern, the Pol pattern and the Pol pattern seen through a polarizer.

tank, allowing remote viewing and recording of the animal's movements. The apparatus was illuminated with four fluorescent lamps outside the cylinder that provided homogeneous lighting of the patterns. The entire apparatus was covered by a black curtain to prevent cuttlefish from using distal cues or being disturbed during the experiments. We tested two patterns (Fig. 1B) of alternating stripes 1 cm wide, each covering 6.3 deg of an arc when viewed from the edge of the holding tank. One pattern consisted of black (0), dark grey (65), white (255) and light grey (190) stripes (BWG pattern; Fig. 1B). The other pattern consisted of polarized stripes with alternating horizontal, 45 deg, vertical and 135 deg orientations of linear polarization (Pol pattern; Fig. 1B) [for further details, see Darmaillacq and Shashar (Darmaillacq and Shashar, 2008)]. A sheet of white paper was used as a negative control.

Optomotor test

The experiment started 5 min after the introduction of a cuttlefish into the central holding tank to allow it to calm and settle down. Each pattern was rotated at four angular velocities (30, 60, 100 and 130 deg s⁻¹) in both clockwise and counter-clockwise directions. In preliminary experiments using patterns, these speeds ranged from those that elicited a clear positive response (OMR 30–100 deg s⁻¹) to one that no longer elicited any response (130 deg s⁻¹). During a trial, when the cuttlefish followed the direction and speed of the rotating pattern (OMR) with the rotation of their whole body for at least 180 deg or just with their eyes for at least four back-and-forth motions in the proper direction, the response was considered positive (see supplementary material Movie 1). In this case, the cylinder was stopped to avoid habituation or fatigue. Otherwise the response was considered negative and the trial ended after 1 min (see supplementary material Movie 2). Each cuttlefish was tested once, in a continuous session consisting of 16 experimental trials (two patterns × four rotation velocities × two rotation directions) and eight control trials with the white sheet (totaling 24 trials). The pattern used for the first eight trials was chosen randomly. Then, trials were performed with the four rotation velocities presented in a random order. For each velocity, two consecutive trials were performed, alternating the directions of rotation. In the next eight trials, the pattern was switched and tested as described above. Lastly, the white sheet was used to perform negative control trials for each velocity and direction. The inter-trial interval between speeds and directions using the same pattern was 1 min; the inter-trial interval between patterns was 5 min.

Only animals that did not respond to the control presentation and responded to both rotational directions were considered as showing an overall positive response. This requirement may be somewhat harsh as some animals showed a clear handedness preference, responding stronger or exclusively to one handedness of presentation than to another (see also Darmaillacq and Shashar, 2008); as a consequence, the cuttlefish that exhibited handedness were included in the analysis but they were not scored with an overall positive response. None of the cuttlefish responded to the negative control, hence all were included in the analysis.

We used 60 cuttlefish. Ten animals were tested at each age (0, 6, 12, 18, 24 and 30 days). The dorsal mantle length of each cuttlefish was measured after the test.

Experiment 2: importance of polarization in prey preference and detection

Prey

In both tests, two types of prey were used: mysid shrimp (*Neomysis integer*), which show low luminance contrast and high polarization contrast, and crabs (*Carcinus maenas*), which show high luminance

contrast and little or no polarization contrast as examined with an imaging polarimeter (N.S., unpublished data). Mysid shrimp were reared at the CREC and were returned there after tests. Crabs were collected at low tide under rocks and were used to feed other cuttlefish after the tests.

Choice test

The experimental apparatus was a V-shaped arena made of grey PVC (15×10×6 cm, length × width × depth; Fig. 2). Two glass tubes (4 cm diameter and 6 cm high), each containing five prey of the same species, were placed opposite to the corner and were illuminated from above by an LED spotlight. One of the tubes was a glass tube transparent to light luminance and polarization information (Pol tube). The other was a glass tube covered with plastic film transparent to light luminance information but that distorted polarization information (DePol tube), as examined using two Polaroid HN38S linear polarizing filters (Shashar et al., 2000). The position (left or right) of the tubes was randomly distributed among cuttlefish. Tubes were occluded by an opaque cover before the beginning of the test. The cuttlefish was gently transferred from the housing tank to the apparatus. It positioned itself in the corner of the V, the head facing the tubes. The cuttlefish had 15 min to settle down and acclimatize to the apparatus. The opaque cover was then removed and the cuttlefish was given 5 min to attack the prey contained in one of the tubes. At the end of the test, the cuttlefish was put back in an individual rearing tank and fed shrimp, *Crangon crangon*.

Cuttlefish were tested at the age of 7 days ($N=36$) and 30 days ($N=36$). For each age, 18 cuttlefish were presented with mysid

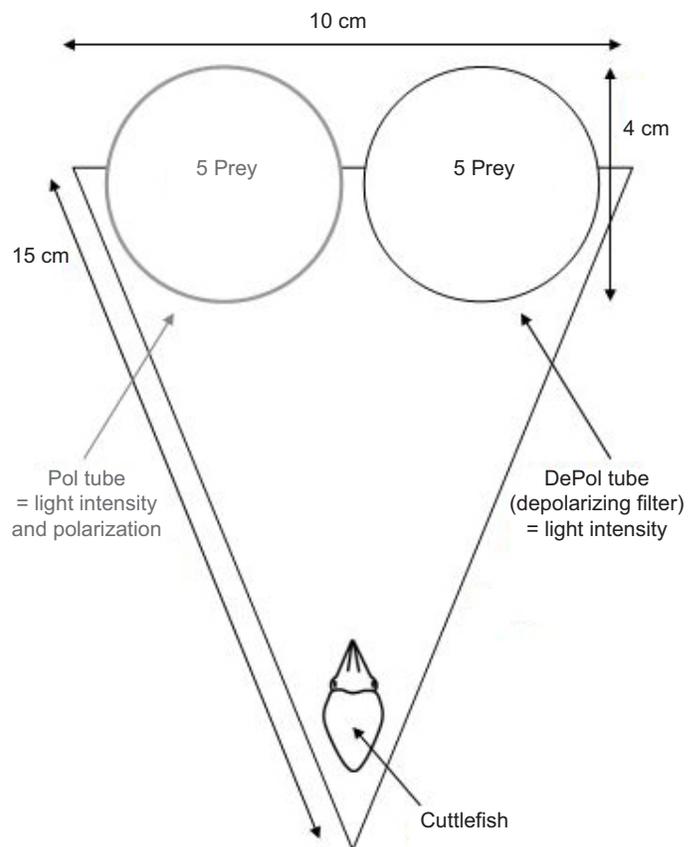


Fig. 2. Apparatus for choice test. Prey items were mysid shrimp or crabs placed in a transparent tube that let through only light luminance (DePol tube) or light luminance and contrast (Pol tube).

shrimp and the other 18 with crab. Each cuttlefish was tested only once. The cuttlefish choice was recorded. An attack was recorded when the cuttlefish shot its tentacles towards a tube containing mysid shrimp or jumped on a tube containing crabs.

Latency test

This test was designed to check that cuttlefish were able to detect prey in a DePol tube and to compare the detection latencies in both conditions (Pol or DePol).

The experimental apparatus was a V-shaped arena made of grey PVC (15×6×6 cm, length × width × depth). One tube (Pol or DePol) containing five prey items was placed at the opposite of the corner. Each cuttlefish was tested successively with the Pol tube and the DePol tube presented in a random order with 5 h between presentations, during which time cuttlefish were returned to their home tank. The acclimation procedure was the same as the one described above. The latency of prey detection was recorded. The detection was assessed by the binocular convergence of the cuttlefish eyes and the positioning of the arms pointed towards the prey (Messenger, 1973). Cuttlefish were tested at the age of 7 days ($N=36$) and 30 days ($N=36$). For each age, half of the cuttlefish were presented with mysid shrimp and half with crab.

Statistical analysis

Data were analyzed using StatXact 7 (Cytel Studio Software, Cambridge, MA, USA). All analyses used a significance threshold of $\alpha=0.05$. Pearson's chi-square tests were used to compare the percentage of cuttlefish showing an OMR with the same pattern between the different ages. If the null hypothesis was rejected, Fisher's exact tests were used for *post hoc* pairwise comparisons. McNemar's tests were used to compare the percentage of cuttlefish showing an OMR at the same speed and age between the two different patterns (Siegel and Castellan, 1988). Permutation tests were used to compare the detection latencies. The preference for attacking prey in the polarization or luminance contrast condition was analysed with chi-square exact tests. Fisher's exact test was used to examine whether preference differed between prey groups and between age groups.

RESULTS

Experiment 1: OMR to luminance versus polarization contrast patterns

When presented with an intensity pattern (BWG), the percentage of cuttlefish showing an OMR at a rotating velocity of 30 and 60 deg s^{-1} did not significantly vary with age (30 deg s^{-1} , $\chi^2_5=10.34$, $P=0.2$; 60 deg s^{-1} , $\chi^2_5=7.451$, $P=0.3$; Fig. 3). At 30 deg s^{-1} , this percentage was already very high at hatching (80%) and then reached 100% at 6 days. At 60 deg s^{-1} , 60% of the cuttlefish showed an OMR at hatching and 6 days of age and 100% was observed from 24 days. At a velocity of 100 deg s^{-1} , the percentage of cuttlefish showing an OMR significantly increased from 10% at hatching to 90% at 30 days ($\chi^2=12.8$, $P=0.001$). At the control velocity of 130 deg s^{-1} , none of the cuttlefish showed an OMR, regardless of age.

With the Pol pattern, the percentage of cuttlefish showing an OMR increased at each velocity with age (30 deg s^{-1} , $\chi^2_5=21.67$, $P=0.0003$; 60 deg s^{-1} , $\chi^2_5=11.67$, $P=0.04$; 100 deg s^{-1} , $\chi^2_5=17.92$, $P=0.003$). At 30 deg s^{-1} , 20% of the cuttlefish responded at hatching and the percentage increased to reach 100% at 30 days ($\chi^2=13.33$, $P<0.001$). At 60 deg s^{-1} , the percentage increased from 10% of the cuttlefish showing an OMR at hatching to 80% at 30 days ($\chi^2=9.899$, $P=0.006$). At 100 deg s^{-1} , none of the cuttlefish showed an OMR at hatching and 6 days, but the percentage of cuttlefish responding reached 60% at 30 days ($\chi^2=8.571$, $P=0.01$).

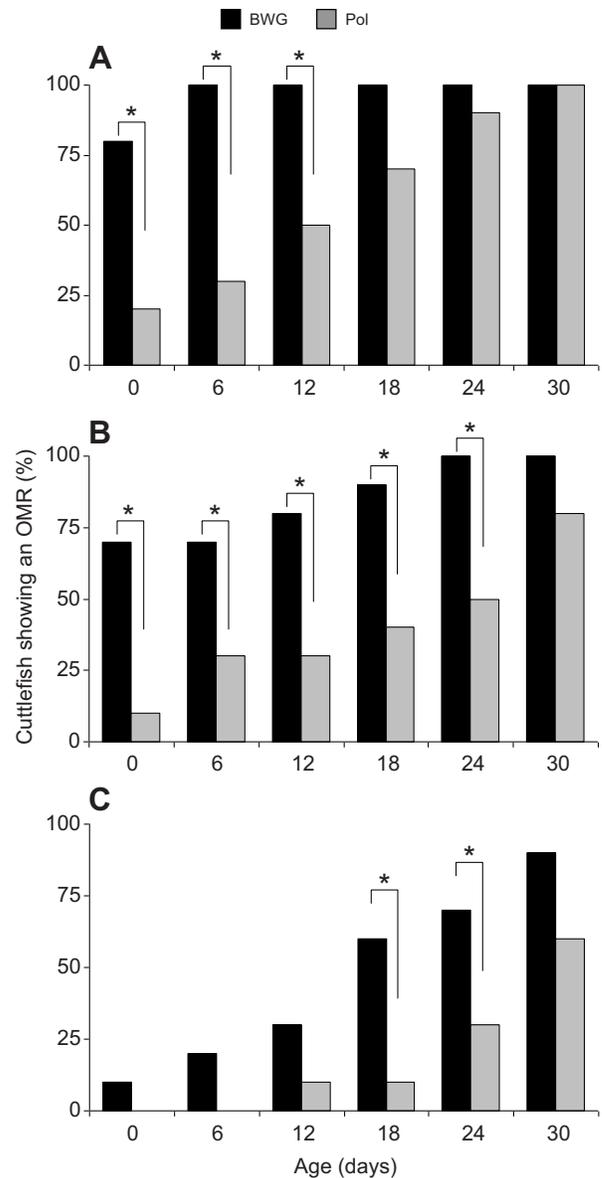


Fig. 3. Percent of the cuttlefish ($N=10$ per group) that showed an optomotor response (OMR) to BWG (luminance only; black) or Pol (polarization; grey) patterns rotating at velocities of (A) 30, (B) 60 and (C) 100 deg s^{-1} . Asterisks indicate a significant difference in the percentage of cuttlefish showing an OMR between the BWG and Pol patterns (McNemar's test, $P<0.05$).

The two patterns did not elicit the same percentage of cuttlefish showing an OMR. Indeed, at the rotating velocity of 30 deg s^{-1} , fewer cuttlefish responded to the Pol pattern than to the BWG pattern at hatching, 6 and 12 days (hatching, $P=0.004$; 6 days, $P=0.007$; 12 days, $P=0.026$). From 18 to 30 days, these percentages were no longer significantly different (18 days, $P=0.1$; 24 days, $P=0.5$). At the velocity of 60 deg s^{-1} , fewer cuttlefish showed an OMR to the Pol pattern than to the BWG one from hatching to 24 days (hatching, $P=0.007$; 6 days, $P=0.05$; 12, 18 and 24 days, $P=0.026$). At 100 deg s^{-1} , the percentage of cuttlefish showing an OMR to the Pol and BWG patterns was low and did not differ from hatching to 12 days (hatching, $P=0.5$; 6 and 12 days, $P=0.2$). More cuttlefish responded to the BWG than to the Pol pattern at 18 and 24 days of age ($P=0.026$ and $P=0.05$, respectively).

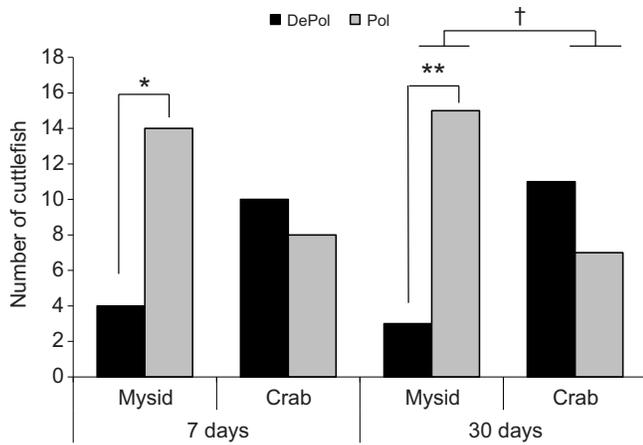


Fig. 4. Preference between prey by 7- and 30-day-old cuttlefish. Prey items were either mysid shrimp or crabs presented either in the DePol tube (black) or the Pol tube (grey). * $P < 0.05$; ** $P < 0.01$ chi-square exact test, † $P < 0.05$ Fisher's exact test.

Experiment 2: importance of polarization in prey preference and detection

Choice test

At 7 and 30 days after hatching, cuttlefish more frequently attacked mysid shrimp in the Pol tube than in the DePol tube (7 days, $\chi^2 = 5.6$, $P = 0.03$; 30 days, $\chi^2 = 8$, $P = 0.008$; Fig. 4), but did not attack crabs in either tube significantly more often (7 days, $\chi^2 = 0.2$, $P = 0.8$; 30 days, $\chi^2 = 0.8$, $P = 0.5$). At 30 days, cuttlefish significantly preferred mysid shrimp in the Pol tube to shrimp in the DePol tube: in contrast, they had no preference for crab whether they were placed in the Pol or DePol tubes ($\chi^2 = 7.5$, $P = 0.015$).

Latency test

At 7 days of age, cuttlefish detected mysid shrimp faster when placed in the Pol tube than in the DePol tube ($P = 0.0006$; Fig. 5). At 30 days, the latency of detection did not significantly differ between conditions ($P = 0.59$). In both conditions, cuttlefish detected mysid shrimp faster at 30 days than at 7 days (shrimp in a Pol tube, $P = 0.04$; in a DePol tube, $P < 0.001$; Fig. 5). At both 7 and 30 days of age, there was no difference in the latency of detection for crabs placed in the Pol tube or in the DePol tube (7 days, $P = 0.95$; 30 days, $P = 0.72$). However, cuttlefish detected the crabs faster at 30 days than at 7 days in both conditions (crabs in a DePol tube, $P = 0.012$; in a Pol tube, $P = 0.006$; Fig. 5).

DISCUSSION

In the first experiment, most of the cuttlefish showed an OMR to the luminance (BWG) pattern rotating from hatching at the lowest velocity (30 deg s^{-1}), where each stripe covered 6.3 deg of an arc. This result is in accordance with the findings of Groeger et al. (Groeger et al., 2005): under well-illuminated conditions, newly hatched cuttlefish detected stripes covering at least 2.5 deg of an arc. At higher velocities, nearly all animals detected and followed the pattern at 30 days of age (Fig. 3). These results suggest that the temporal resolution of juvenile contrast sensitivity increases with age. The polarization sensitivity develops more slowly. Indeed, only few newly hatched cuttlefish showed an OMR to the Pol pattern at the low velocities of 30 and 60 deg s^{-1} . The number of responding cuttlefish slowly increased with age. Further, the responses at young ages were stronger at the low rotation speeds (30 and 60 deg s^{-1}) than the faster one (100 deg s^{-1}), but this was not the case with the

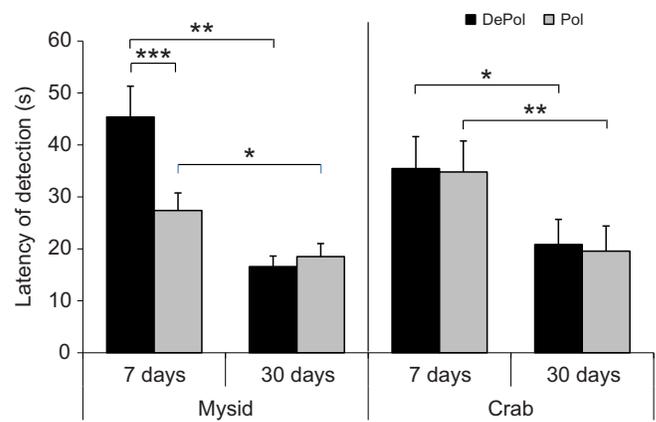


Fig. 5. Mean (\pm s.e.m.) latency (s) of prey detection by 7- and 30-day-old cuttlefish. Prey items were mysid shrimp or crabs presented in the DePol tube (black) or the Pol tube (grey). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ permutation test.

older cuttlefish (except for the 130 deg s^{-1} rotation speed). These results suggest a maturation of the temporal resolution for polarization input as well. At 30 days, at least half of the cuttlefish responded to the polarization pattern at all velocities, except for the highest rotation rate of 130 deg s^{-1} (Fig. 3). Previous studies demonstrated an OMR to polarized stripes in other mature cuttlefish species, using a velocity of 12 deg s^{-1} and with stripes 2.5 cm in width (Talbot and Marshall, 2010a; Talbot and Marshall, 2010b), which raises the possibility that our cuttlefish would have responded to slower rotating patterns as well. However, Darmaillacq and Shashar (Darmaillacq and Shashar, 2008) did not succeed in eliciting an OMR to a polarized pattern in adult *Sepia elongata*, using velocities ranging from 34 to 178 deg s^{-1} , although *S. elongata* possess orthogonal photoreceptors in their retina suggesting the ability for polarization detection. In animals that are known to see colors, patterns composed of two colored stripes of equal luminance do not necessarily elicit OMR (Schaerer and Neumeyer, 1996; Anstis et al., 1998; Krauss and Neumeyer, 2003). Therefore, other techniques of investigations were needed to determine whether the ability for PS does exist in newly hatched cuttlefish. For this purpose, we used a biologically relevant context: prey detection and attack.

In the second experiment, 7-day-old cuttlefish preferred to attack mysid shrimp when polarization information was available (Pol tube; Fig. 4). Detection of mysid shrimp was faster when contained in the Pol tube rather than in the DePol tube (Fig. 5). In 30-day-old cuttlefish, we still observed this preference but cuttlefish did not detect mysid shrimp faster in the Pol tube. Indeed, detection latency of mysid shrimp when placed in the DePol tube improved. On the contrary, 7- and 30-day-old cuttlefish did not show a preference for crab in Pol and DePol tubes, and the latency of detection was the same in both conditions. In addition, the latency of detection decreased with age. These results suggest a hierarchical order of image processing. When the prey is highly luminance contrasted, such as the crab, PS is not involved in its detection or recognition. However, when luminance contrast is low (such as with the mysid shrimp), PS kicks in. PS has been shown to enhance the detection of transparent prey in squid paralarvae (Shashar et al., 1998). Dickel et al. (Dickel et al., 1997) showed a rapid increase in triggering of predation on mysid shrimp during the first week of life in cuttlefish. This might suggest a post-embryonic development of PS allowing increase in prey detection and prey-catching success. Our results

confirm that PS helps newly hatched cuttlefish detect transparent prey. Moreover, they show that luminance contrast sensitivity improves during their first month of life. PS overcomes this poor sensitivity in helping cuttlefish be more efficient to detect prey that generate a polarization contrast from their background, such as shrimp.

The results from the second experiment show that polarization was perceived by cuttlefish as young as 7 days of age and that prey detection based on luminance contrast improves with age. Yet the percentage of cuttlefish showing an OMR to the polarization pattern was lower than for the luminance pattern at all ages and velocities of rotation. These apparently puzzling results could be explained by the higher speed of motion for the rotating pattern compared with the nearly stationary prey. In such a case, using a slowly moving pattern (Talbot and Marshall, 2010a; Talbot and Marshall, 2010b) might elicit stronger responses even in very young animals. Alternatively, these apparently contradicting results can be due to differences in the size of the receptive fields of the retina needed to detect each type of signal. At least two photoreceptors are needed to detect motion based on luminance differences alone. However, for simple polarization detection (without motion), at least two photoreceptors with their microvilli oriented orthogonally to each other are needed (Wehner, 2001; Horvath and Varju, 2004; Marshall and Cronin, 2011). Therefore, it is likely that more photoreceptors should be necessary for polarization-based motion detection than for luminance-based motion detection. Another hypothesis is that polarization and luminance signals are processed separately and may have different roles in vision. Polarization contrast could be more useful to detect the shape of the prey than to detect motion, although it could have a function in both, as well as in other tasks. In insects, or at least in locusts, polarized and unpolarized information are coded differently and are processed by different type of neurons in the optic lobe (Labhart and Meyer, 2002; Pfeiffer et al., 2005). In cephalopods, little is known about the coding of luminance and polarization information in the optic lobe. However, the current behavioral observations and previous ones (Grable et al., 2002) suggest that polarization is not a simple modulation of luminance information, but rather that it is processed as a distinct channel of visual information. Further studies using electrophysiological and immunochemistry procedures are needed to determine the neural pathways for polarization and luminance information processing.

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AUTHOR CONTRIBUTIONS

This work is part of L.C.'s PhD thesis. L.C. reared the cuttlefish, ran the experiments, participated in the interpretation of the findings and drafted the article. N.S. provided the optomotor apparatus and the basic methods to use it, and contributed to the interpretation of the findings regarding polarization and to the revisions. L.D. and A.-S.D. had the original idea and designed the experiment; they both participated in the interpretation of the findings. L.D. supervised L.C.'s work and A.-S.D. made substantial contributions to the revisions of the article.

COMPETING INTERESTS

No competing interests declared.

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REFERENCES

- Anstis, S., Hutahajan, P. and Cavanagh, P. (1998). Optomotor test for wavelength sensitivity in guppyfish (*Poecilia reticulata*). *Vision Res.* **38**, 45-53.
- Boal, J. G., Shashar, N., Grable, M. M., Vaughan, K. H., Loew, E. R. and Hanlon, R. T. (2004). Behavioral evidence for intraspecific signaling with achromatic and polarized light by cuttlefish (Mollusca: Cephalopoda). *Behaviour* **141**, 837-861.
- Boletzky, S., Nixon, M. and Messenger, J. B. (1977). Post-hatching behaviour and mode of life in cephalopods. In *The Biology of cephalopods: the proceedings of a symposium held at the Zoological Society of London No. 38* (ed. M. Nixon, J. B. Messenger and Zoological Society of London), pp. 557-567. London: Academic Press.
- Brown, P. K. and Brown, P. S. (1958). Visual pigments of the octopus and cuttlefish. *Nature* **182**, 1288-1290.
- Cartron, L., Darmaillacq, A.-S., Jozet-Alves, C., Shashar, N. and Dickel, L. (2012). Cuttlefish rely on both polarized light and landmarks for orientation. *Anim. Cogn.* **15**, 591-596.
- Carvalho, P. S. M., Noltie, D. B. and Tillitt, D. E. (2002). Ontogenetic improvement of visual function in the medaka *Oryzias latipes* based on an optomotor testing system for larval and adult fish. *Anim. Behav.* **64**, 1-10.
- Cronly-Dillon, J. R. and Muntz, W. R. (1965). The spectral sensitivity of the goldfish and the clawed toad tadpole under photopic conditions. *J. Exp. Biol.* **42**, 481-493.
- Dacke, M., Doan, T. A. and O'Carroll, D. C. (2001). Polarized light detection in spiders. *J. Exp. Biol.* **204**, 2481-2490.
- Darmaillacq, A.-S. and Shashar, N. (2008). Lack of polarization optomotor response in the cuttlefish *Sepia elongata* (d'Orbigny, 1845). *Physiol. Behav.* **94**, 616-620.
- Darmaillacq, A.-S., Chichery, R., Shashar, N. and Dickel, L. (2006). Early familiarization overrides innate prey preference in newly hatched *Sepia officinalis* cuttlefish. *Anim. Behav.* **71**, 511-514.
- Darmaillacq, A.-S., Lesimple, C. and Dickel, L. (2008). Embryonic visual learning in the cuttlefish, *Sepia officinalis*. *Anim. Behav.* **76**, 131-134.
- Dickel, L., Chichery, M. P. and Chichery, R. (1997). Postembryonic maturation of the vertical lobe complex and early development of predatory behavior in the cuttlefish (*Sepia officinalis*). *Neurobiol. Learn. Mem.* **67**, 150-160.
- Dickel, L., Boal, J. G. and Budelmann, B. U. (2000). The effect of early experience on learning and memory in cuttlefish. *Dev. Psychobiol.* **36**, 101-110.
- Fuiman, L. A. and Magurran, A. E. (1994). Development of predator defences in fishes. *Rev. Fish Biol. Fish.* **4**, 145-183.
- Gall, M. D. and Fernández-Juricic, E. (2010). Visual fields, eye movements, and scanning behavior of a sit-and-wait predator, the black phoebe (*Sayornis nigricans*). *J. Comp. Physiol. A* **196**, 15-22.
- Glantz, R. M. (2001). Polarization analysis in the crayfish visual system. *J. Exp. Biol.* **204**, 2383-2390.
- Grable, M. M., Shashar, N., Gilles, N. L., Chiao, C.-C. and Hanlon, R. T. (2002). Cuttlefish body patterns as a behavioral assay to determine polarization perception. *Biol. Bull.* **203**, 232-234.
- Groeger, G., Cotton, P. and Williamson, R. (2005). Ontogenetic changes in the visual acuity of *Sepia officinalis* measured using the optomotor response. *Can. J. Zool.* **83**, 274-279.
- Guibé, M., Poirel, N., Houdé, O. and Dickel, L. (2012). Food imprinting and visual generalization in embryos and newly hatched cuttlefish, *Sepia officinalis*. *Anim. Behav.* **84**, 213-217.
- Hanlon, R. T. and Messenger, J. B. (1996). *Cephalopod Behaviour*. Cambridge: Cambridge University Press.
- Horvath, G. and Varju, D. (2004). *Polarized Light in Animal Vision: Polarization Patterns in Nature*. Berlin: Springer-Verlag.
- Johnsen, S., Marshall, N. J. and Widder, E. A. (2011). Polarization sensitivity as a contrast enhancer in pelagic predators: lessons from *in situ* polarization imaging of transparent zooplankton. *Philos. Trans. R. Soc. B* **366**, 655-670.
- Kaiser, W. (1974). The spectral sensitivity of the honeybee's optomotor walking response. *J. Comp. Physiol. A* **90**, 405-408.
- Kiltie, R. A. (2000). Scaling of visual acuity with body size in mammals and birds. *Funct. Ecol.* **14**, 226-234.
- King, R. B., Douglass, J. K., Phillips, J. B. and Baube, C. L. (1993). Scotopic spectral sensitivity of the optomotor response in the green treefrog *Hyla cinerea*. *J. Exp. Zool.* **267**, 40-46.
- Krauss, A. and Neumeyer, C. (2003). Wavelength dependence of the optomotor response in zebrafish (*Danio rerio*). *Vision Res.* **43**, 1275-1284.
- Labhart, T. and Meyer, E. P. (2002). Neural mechanisms in insect navigation: polarization compass and odometer. *Curr. Opin. Neurobiol.* **12**, 707-714.
- Luczkovich, J. J. (1988). The role of prey detection in the selection of prey by pinfish *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* **123**, 15-30.
- Marshall, J. and Cronin, T. W. (2011). Polarisation vision. *Curr. Biol.* **21**, R101-R105.
- Marshall, N. J. and Messenger, J. B. (1996). Colour-blind camouflage. *Nature* **382**, 408-409.
- Mäthger, L. M., Barbosa, A., Miner, S. and Hanlon, R. T. (2006). Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. *Vision Res.* **46**, 1746-1753.
- Mäthger, L. M., Shashar, N. and Hanlon, R. T. (2009). Do cephalopods communicate using polarized light reflections from their skin? *J. Exp. Biol.* **212**, 2133-2140.
- McCann, G. D. and Arnett, D. W. (1972). Spectral and polarization sensitivity of the dipteran visual system. *J. Gen. Physiol.* **59**, 534-558.
- McCann, G. D. and MacGinitie, G. F. (1965). Optomotor response studies of insect vision. *Proc. R. Soc. Lond. B* **163**, 369-401.
- Messenger, J. B. (1973). Learning in the cuttlefish, *Sepia*. *Anim. Behav.* **21**, 801-826.
- Moody, M. F. and Parriss, J. R. (1960). The visual system of *Octopus*. Discrimination of polarized light by octopus. *Nature* **186**, 839-840.
- Moody, M. F. and Parriss, J. R. (1961). The discrimination of polarized light by *Octopus*: a behavioural and morphological study. *Z. Vgl. Physiol.* **44**, 268-291.

- Neave, D. (1984). The development of visual acuity in larval plaice (*Pleuronectes platessa* L.) and turbot (*Scophthalmus maximus* L.). *J. Exp. Mar. Biol. Ecol.* **78**, 167-175.
- Pankhurst, P. M., Pankhurst, N. W. and Montgomery, J. C. (1993). Comparison of behavioural and morphological measures of visual acuity during ontogeny in a teleost fish, *Forsterygion varium*, Tripterygiidae (Forster, 1801). *Brain Behav. Evol.* **42**, 178-188.
- Pfeiffer, K., Kinoshita, M. and Homberg, U. (2005). Polarization-sensitive and light-sensitive neurons in two parallel pathways passing through the anterior optic tubercle in the locust brain. *J. Neurophysiol.* **94**, 3903-3915.
- Philipsborn, A. and Labhart, T. (1990). A behavioural study of polarization vision in the fly, *Musca domestica*. *J. Comp. Physiol. A* **167**, 737-743.
- Poirier, R., Chichery, R. and Dickel, L. (2004). Effects of rearing conditions on sand digging efficiency in juvenile cuttlefish. *Behav. Processes* **67**, 273-279.
- Poirier, R., Chichery, R. and Dickel, L. (2005). Early experience and postembryonic maturation of body patterns in cuttlefish (*Sepia officinalis*). *J. Comp. Psychol.* **119**, 230-237.
- Rahmann, H., Jeserich, G. and Zeutzius, I. (1979). Ontogeny of visual acuity of rainbow trout under normal conditions and light deprivation. *Behaviour* **68**, 315-322.
- Rinner, O., Rick, J. M. and Neuhauss, S. C. F. (2005). Contrast sensitivity, spatial and temporal tuning of the larval zebrafish optokinetic response. *Invest. Ophthalmol. Vis. Sci.* **46**, 137-142.
- Schaerer, S. and Neumeier, C. (1996). Motion detection in goldfish investigated with the optomotor response is 'color blind'. *Vision Res.* **36**, 4025-4034.
- Shashar, N., Rutledge, P. and Cronin, T. W. (1996). Polarization vision in cuttlefish in a concealed communication channel? *J. Exp. Biol.* **199**, 2077-2084.
- Shashar, N., Hanlon, R. T. and Petz, A. D. (1998). Polarization vision helps detect transparent prey. *Nature* **393**, 222-223.
- Shashar, N., Hagan, R., Boal, J. G. and Hanlon, R. T. (2000). Cuttlefish use polarization sensitivity in predation on silvery fish. *Vision Res.* **40**, 71-75.
- Siegel, S. and Castellan, N. J. (1988). *Nonparametric Statistics for the Behavioral Sciences*, 2nd edn. New York, NY: McGraw-Hill.
- Stevens, M. and Merilaita, S. (2009). Animal camouflage: current issues and new perspectives. *Philos. Trans. R. Soc. B* **364**, 423-427.
- Talbot, C. M. and Marshall, J. (2010a). Polarization sensitivity in two species of cuttlefish – *Sepia plangon* (Gray 1849) and *Sepia mestus* (Gray 1849) – demonstrated with polarized optomotor stimuli. *J. Exp. Biol.* **213**, 3364-3370.
- Talbot, C. M. and Marshall, J. (2010b). Polarization sensitivity and retinal topography of the striped pyjama squid (*Sepioloidea lineolata* Quoy/Gaimard 1832). *J. Exp. Biol.* **213**, 3371-3377.
- Tauber, E. S. and Koffler, S. (1966). Optomotor response in human infants to apparent motion: evidence of innateness. *Science* **152**, 382-383.
- Temple, S. E., Pignatelli, V., Cook, T., How, M. J., Chiou, T. H., Roberts, N. W. and Marshall, N. J. (2012). High-resolution polarisation vision in a cuttlefish. *Curr. Biol.* **22**, R121-R122.
- Todd, P. A., Briers, R. A., Ladle, R. J. and Middleton, F. (2006). Phenotype-environment matching in the shore crab (*Carcinus maenas*). *Mar. Biol.* **148**, 1357-1367.
- Wehner, R. (2001). Polarization vision – a uniform sensory capacity? *J. Exp. Biol.* **204**, 2589-2596.
- Wells, M. J. (1962). *Brain and Behavior in Cephalopods*. Stanford, CA: Stanford University Press.
- Wolf, R., Gebhardt, B., Gademann, R. and Heisenberg, M. (1980). Polarization sensitivity of course control in *Drosophila melanogaster*. *J. Comp. Physiol. A* **139**, 177-191.